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Low-Dimensional Control: Tonus (1963)

Onno G. Meijer, Yakov M. Kots, and V. Reggie Edgerton

In 1963, an article on "Tonus" (tone), written by Nikolai A. Bernstein and Yakov M. Kots, appeared in the second edition of the *Bols'aja Medicinskaja Enciclopedija* [Grand Medical Encyclopedia]. The paper is now published for the first time in the English language, with Mark L. Latash as translator. In accordance with then contemporary neurophysiology and neuropsychology, the paper presented "tone" as a graded phenomenon (as opposed to all-or-none), serving to prepare the segmental level for phasic contractions. Influenced by Granit and Matthews, the authors proposed that the suprasegmental level controls the threshold and the slope of the stretch reflex. In their introduction to the present edition, the editors understand this proposal in the context of low-dimensional control, that is, control in terms of one or a few variables (as opposed to central commands specifying all the details). Selected episodes from the history of low dimensional control and its logical counterpart, spinal intelligence, are used to illustrate how difficult these ideas were to accept. As so often in new scientific developments, confusion was the rule, and in this respect the paper on "Tonus" is no exception. In the epilogue, Kots gives his personal memories of the context in which the paper was written. At the time, he was working on "equitonometry" (equi-tono-metry), measuring tonic balance with gravity eliminated. Results of equitonometric research quite naturally led to the idea that suprasegmental centers control the threshold and the slope of the tonic stretch reflex. As Kots remembers, that was "no big deal."

Key Words: N.A. Bernstein, neuromuscular tone, low-dimensional control, equilibrium-point hypothesis, spinal intelligence, central pattern generators

In the late 1950s, Nikolai Bernstein was invited to write an article on "Tonus" (Tone) for the second edition¹ of the *Bols'aja Medicinskaja Enciclopedija*

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¹For the first edition, he had written the article on "Movements" (1929, in: Fel'dman & Meijer, 1999). In the second edition, "Movements" was written by another author.

[Grand Medical Encyclopedia]. He then asked one of us (Y.M.K.) to write the paper with him. Just as in his earlier contributions to the Encyclopedia (cf. Beek & Meijer, 1999; Fel'dman & Meijer, 1999), Bernstein refrained from a cut and dry summing up of established knowledge, wanting to hint instead at new theoretical developments and concepts. Maybe he thought it safer to first publish revolutionary ideas in a politically innocent medium; or maybe he just liked to involve the general public in the development of his thinking, great popularizer of ideas as he was (Feigenberg & Meijer, 1999; cf. Bernstein, 1945–1946/1996). In our opinion, “Tonus” hints at low-dimensional control in a way that was new at the time. In this respect, it may be important to note that Bernstein (e.g., 1935/1967) played an important role in the history of low-dimensional control, that is, control in terms of one or a few variables, the details being filled-in by the lower levels² (cf. Greene, 1972; Turvey, 1977).

Of course, the paper on “Tonus” contains language that sounds archaic by now,³ but still, we think the text is fascinating also today. The paper begins by defining *tone* as the “controlled totality of the characteristics of the neuromuscular apparatus and of the mechanical parameters of the muscle,” one of Bernstein’s didactically brilliant overstatements⁴ that set the stage. Tone is linked to then-contemporary developments in neurophysiology (cf. Bishop, 1956) and neuropsychology (e.g., Pribram, 1971). First, the “all or none law” for the action potential is understood as a relatively late exception in the evolution of the nervous system; normal reactions are graded, and so apparently is the organization of tone. Second, the locomotor apparatus must be in a continuous state of preparedness, and tone prepares the system for phasic contractions.

Tone is modulated via the pathways that mediate the stretch reflex. Generally, “reflexes” had been seen as stereotyped reactions—Bernstein spent much of his life fighting the (neo)Pavlovian notion of reflex (Pickenhain, 1998; Meijer, in press b)—but in the paper, tone is depicted as a self-organized phenomenon under constraints from the brain. Stereotypy of reflex action is implicitly rejected: “Central regulation does not become manifest in a continuous reflex contraction of muscles but in reactions that occur in response to changes in a muscle’s length.” In the paper, the consequences of this idea are not worked out in any detail, nor was the idea as such new at the time,⁵ but it appears to have important implications. What the brain does in motor control is modifying the sensitivity of the segmental

²In his 1935 paper (1935/1967), Bernstein was not entirely consistent as to the way the details are filled-in (cf. Bongardt & Meijer, 2000). Interestingly, the paper on “Tonus” appears to have problems in that respect as well.

³Such as the distinction between *paleokinetic* and *neokinetic* (see below), and the emphasis on the need for the neuromuscular system to be “prepared” for phasic contractions. Historiographically, however, it is important to emphasize that being archaic does not necessarily imply being wrong or useless.

⁴Bernstein appears to have been fond of hyperbolic statements in his *Encyclopedia* articles. In 1929, for instance, he wrote: “There are no situations in which muscle shortening is the cause of a movement” (Fel’dman & Meijer, 1999, p. 119); in 1930: “No movement can be entirely planned from its very beginning” (Beek & Meijer, 1999, p. 5). So, maybe the opening statement of the presently edited paper should not be seen as a “definition” of tone but rather as an invitation for the reader to regard “tone” as an interesting topic.

⁵To the best of our knowledge, it was Sherrington (1906; cf. Latash, 1993) who introduced the idea that the parameters of muscle reflexes are under central control.

level to specific sensory information.⁶ The periphery can then deal intelligently with that information (for instance, by reaching a specific position even, within limits, in the presence of perturbations).⁷ Apparently, such intelligence need not come from the brain. To date, we would argue that much of the detail derives from the circular (network) organization of sensory-motor pathways at the segmental level (cf. Edgerton et al., 1997a), and the non-linearity of relationships throughout the system (cf. Fel'dman, 1966b).

After the above introduction, mainly written by Bernstein, the second author of the paper⁸ presents an overview of segmental mechanisms, very much along the lines of Granit (e.g., 1955)⁹ and Matthews (e.g., 1958a, 1958b). And then, quite naturally following from the preceding but still unexpected, we read that suprasegmental centers control the threshold and the gain (the slope of the length tension diagram) of the stretch reflex. Clearly, this statement belongs to the neurophysiology of its time.¹⁰ At the same time, one can read it as referring to the dimensionality of the central command (cf. Bernstein, 1935/1967), quite in the spirit of the equilibrium-point hypothesis (Asatryan & Fel'dman, 1965; Fel'dman, 1966a, 1966b; cf. Feldman, 1966). In our opinion, the paper on "Tonus" is one step on the way to low-dimensional control. With hindsight, we can recognize that this was not completely understood by its authors at the time. One can read, for instance, that suprasegmental control defines "the magnitude of the afferent excitatory inflow," which appears to be slightly off the mark, and that tone defines "the compound

⁶Modern literature goes much further in this respect, since it was discovered that even the sign of a reflex can change depending on the phase of a cyclic action such as walking (Forssberg, Grillner, & Rossignol, 1975).

⁷For Bernstein's 1930 understanding of the organization of the scratch reflex in spinal frogs, see his 1930 paper on "Coordination" (Beek & Meijer, 1999).

⁸After the initial writing, the two contributions were mixed so that it is now difficult to decide with certainty which statement derived from which author (Y.M.K., personal memory).

⁹In 1955, Granit wrote: "The spindle loop integrates motor and sensory performance in a curious and fascinating manner. The brain drives and sensitizes end organs, which in their turn are capable of driving the muscle which contains these end organs as well as its synergistic muscles. Now, muscle is the instrument of action, and so it seems natural that it should be made to feel the arousal reaction of the animal aroused. Again, considered from the sensory point of view, a purely extrafusal arousal without concomitant γ arousal of the intrafusal fibers of the muscle spindle would make the sense organ pause and consequently be incapable of serving as an 'internal measuring instrument' and hence useless for the animal at the very moment when it is needed" (Granit, 1955, p. 264, quotation marks in the original).

¹⁰Merton's 1953 "servo-hypothesis" stated that the stretch reflex allows a limb to retain its position against an added load. However, the gain of the stretch reflex is too low for this to be an efficient mechanism (cf. Bizzi et al., 1992; Latash, 1993). In 1955, Granit stated: "In many if not most natural contractions hitherto studied the γ loop was first started, the nuclear bag afferents then facilitated, and the appropriate motor neurones and direct activation came last or together with γ activity" (Granit, 1955, p. 268; cf. Kots, 1977, p. 94). Moreover, "the general facilitatory and inhibitory systems of the brain stem are instrumental in determining the level of tonic facilitation through the spindle loop as well as in switching it on and off" (Granit, 1955, p. 261). In 1958, Matthews found that " γ -motoneurons affect the 'threshold' rather than the 'stiffness' of the stretch reflex" (Matthews, 1958a, p. 54P, quotation marks in the original).

amplitude of action potentials," which fails to differentiate between what is controlled and what emerges. It is in the nature of science that those involved in a new development don't grasp its full consequences in a single blow. Thus, the weaknesses of "Tonus" do not diminish its value. To the contrary, they help us understand the checkered history of low-dimensional control and its logical counterpart, spinal intelligence.

The paper emphasizes that tone should no longer be seen as limited to posture. Posture and movement are different aspects of the same organization,¹¹ and at the segmental level there are no specific devices dedicated to either one of them. Finally, methods are mentioned to measure tone. One of these may have sounded particularly intriguing to the reader, that is, "equitonometry": a method to measure tonic muscle balance when the effect of gravity is eliminated. Sure, this was an encyclopedia article, and the reader of "Tonus" is not informed as to the specifics of equitonometry.¹²

After Kuhn's *The Structure of Scientific Revolutions* (1962), one may have come to the belief that new ideas in science arrive in a clean *Gestalt* switch. New developments in science, however, are usually messy, full of misunderstanding, misquotation, and confusion (Fleck, 1935/1980). In the opinion of the present editors, the paper on "Tonus" has all signs of a transition between different modes of thinking and is thus necessarily not entirely consistent. The paper reflects modern neurophysiology of its time, but one can also see it in the context of debates on low-dimensional control and spinal intelligence. These latter topics were, and still are, hard to grasp. We will illustrate that important point with selected episodes from the history of the equilibrium-point hypothesis (low-dimensional control) and the centuries-old debate on the behavior of decerebrate animals (spinal intelligence). The confusion in these episodes should not lessen our respect for the scientists involved. Rather, it should increase our respect for the difficulties the scientific community in question was facing.

Equilibrium-Point Hypotheses

After Feldman launched the equilibrium-point hypothesis (Asatryan & Fel'dman, 1965; Fel'dman, 1966a, 1966b), it took some time to clarify the basic concepts, and thus give maturity to the idea (cf., e.g., Feldman et al., 1998). In the meantime, many authors expressed (dis)agreement—even before it had become sufficiently clear what it was exactly that one (dis)agreed with (for an overview, see Latash, 1993). In fact, the reception of the equilibrium-point hypothesis formed one of the most colorful episodes of 20th century movement science. In the turmoil, statements were rejected that "fly in the face of physiological common sense. Endorsing them would merely transform the alpha model [of the equilibrium-point hypothesis] into a strawman-hypothesis whose refutation could not add anything to our knowledge of motor control" (Bizzi et al., 1992, p. 613). Subsequently, the paper just quoted was accused of not comprehending "the principles of sensorimotor integration underlying the λ model [of the equilibrium-point hypothesis]" and

¹¹For an opposite view, see, e.g., Massion, 1994.

¹²In the present edition, some of these specifics are given in the Epilogue (cf. Kots, 1961 & 1966).

of compounding the "tradition of confusion" (Feldman & Levin, 1995, p. 724). We propose to regard the apparent disagreements as normal signs of birth-pain in a radical break with a tradition that has deep roots in Western¹³ thinking. What was going on?

During a tonic stretch reflex (Liddell & Sherrington, 1924), the muscle behaves as an extended spring that one lets go.¹⁴ Within limits, contracting springs allow for equifinality under transient perturbations.¹⁵ Such equifinality implies, for instance, that during walking the legs can take care of small irregularities on the ground without even involving the nervous system. The (non-linear) spring properties of muscle have attracted considerable attention in the literature, particularly because peripheral equifinality makes central control so much easier (e.g., Asatryan & Fel'dman, 1965; Bizzi et al., 1982; Kelso, 1977; Kelso & Holt, 1980; Kugler & Turvey, 1987; Schmidt, 1982; Van Ingen Schenau & Van Soest, 1996). Nevertheless, identifying the "mass spring model" (Schmidt, 1982, pp. 267-270) with the equilibrium-point hypothesis did confuse the debates. In fact, the equilibrium-point hypothesis assumes spring-like behavior, but such behavior does not define it. Moreover, the spring-like behavior of the joint is mediated "not by active muscles per se . . . but by the whole system, possibly including supraspinal structures" (Feldman & Levin, 1995, p. 728; cf. Feldman, 1986).

A second, related problem had to do with the biological implementation of the control mechanisms in question. Early authors (Granit, 1955; Matthews, 1958a, 1958b; Merton, 1953) took their starting point in then contemporary neurophysiology. Simple hard wiring, however, can never account for intelligence in the spinal cord. The 1963 paper on "Tonus" is ambivalent in this respect. On the one hand, the paper deals with system behavior ("the totality of adjustable controls"); on the other hand, the discussion of the impact of the activity of individual spindles, Golgi tendon organs and so on, suggests some form of micro-determinism. Before the second half of the 1980s, it was not clear that the equilibrium-point hypothesis "indicates an integral measure . . . of the central commands" (Feldman, 1986, p. 25). From our present vantage point, we would like to add that the mammalian spinal cord evolved to recognize routine motor tasks such as scratching, standing, stepping, or even recovering from a stumbling event (Brustein & Rossignol, 1998, 1999), and that it must be the totality of all available information that has meaning to the spinal cord rather than single stimuli from individual afferent fibers.

Such a system view allows for a definition of the equilibrium-point "in accordance with the notion of equilibrium position used in dynamical systems theory"

¹³Of course, the Russian tradition was integrated with what we here call "Western thinking." Unfortunately, the present editors are ignorant about theories on motor coordination and control in, for instance, ancient China or medieval Islam.

¹⁴Bernstein first wrote of the spring properties of muscle in 1926—cf. Latash, 1993, with the following reference: Bernstein, N.A. (1926). *General biomechanics*. Moscow: Medgiz. (In Russian.) Nevertheless, Bernstein had difficulties in integrating muscle properties with his own views on coordination and control (cf., e.g., Bernstein, 1945–1946/1996, pp. 37–41). In Bernstein's Russian 1947 book *On the Construction of Movements* (Moscow: Medgiz), Bernstein depicts a family of muscle characteristics that correspond to different levels of muscle excitation, stating that the central nervous system selects a curve out of the family (M.L. Latash, personal communication, 2000).

¹⁵But not when a constant external load is added (as incorrectly suggested by Merton, 1953).

(Feldman, 1986, p. 34; cf. Andronov & Chaikin, 1949; Haken, 1983; Kelso, 1995). Thus, we have to make do with *processes* that tend toward stable states. In dynamical systems, we may know the dimension of the control parameter but not the exact state at which the system will stabilize. The hallmark, therefore, is self-organized stability. Nevertheless, Bizzi et al. (1982), inspired by Feldman (1966a, 1966b), interpreted the control of goal-directed arm movements in deafferented monkeys as the "selection of a set of length-tension properties in agonist and antagonist muscles, an equilibrium point between the two sets of muscles that correctly position the joint" (Bizzi et al., 1982, p. 139). At first sight (cf. Schmidt, 1982), this appears to be a controlled balance of forces (one spring at each side of the joint), with position emerging, rather than control in terms of position and EMG emerging.

Feldman (1986) coined the understanding of Bizzi et al. the "alpha model" (with the level of muscle activation as control variable), in contrast with his own "lambda model" (positional control, implying that the control variable can be measured in terms of changes in the threshold length, lambda). Were there now indeed two different versions of the equilibrium point hypothesis? In 1992, Bizzi et al. reluctantly agreed that indeed there appeared to be two versions. Their 1992 paper is strangely fascinating. If we counted correctly, the notion "springlike" is used 19 times, 18 of these referring to muscle properties, suggesting a balance of springs around joints with direct control of muscle activation (cf. Schmidt, 1982). Nevertheless, in the summary of the paper, springlike behavior is ascribed to "the neuromuscular system" (Bizzi et al., 1992, p. 603), at least in principle allowing for control in positional terms. Actually, Bizzi et al. argue that experiences with robots reveal that simple force control may lead to instability (cf. Bernstein, 1935/1967). More important, the authors report that electrical stimulation of a specific spot in the premotor area of the spinal cord brings the limb of the spinal frog to a specific place no matter where it starts from. Depending on starting position, each time a different pattern of muscle activation is needed.¹⁶ In our opinion, this is neurophysiological evidence of control in terms of position. Were Bizzi et al. confused, as Feldman and Levin (1995) suggested? Of course they were,¹⁷ but not more so, and not more disturbingly so, than Bernstein and Kots in 1963.

Emotions ran high, and when Mark L. Latash published a book with his own defense of the lambda model, he lamented that writing it was "probably the best way to turn friends into enemies and provoke 'enemies' to even more belligerence" (Latash, 1993, p. x). That is certainly strong language, and once again, we want to ask: What was going on?

¹⁶One of us [O.G.M.] repeated this experiment together with Simon Giszter in Bizzi's lab. It took some time to find the right spot in the premotor area of the spinal cord, but then the behavior of the spinal frog was indeed amazing: Stimulating the same spot at different starting positions of the limb would lead to different patterns of muscle activity so that the limb would reach the same end position (cf. Bizzi, Saltiel, & Tresch, 1998).

¹⁷This may be the right moment to repeat our disclaimer at the end of the preceding section. We are convinced that being confused is an essential part of scientific discovery. For that matter, we cannot even be sure that our own historical reconstruction is free of confusion. We kindly invite the reader to accept our present understanding of debates around low-dimensional control and spinal intelligence as "historiography with a smile."

Decerebrate Animals

Aristotle observed that animal movement is different from that of marionettes because animals can change by themselves (Peck & Foster, 1965, pp. 463-465). In the 16th century, however, Europe started to think differently: Movements are displacements of the skeleton through muscles that passively obey orders from the intelligent soul in, or connected to, the brain (Vesalius, 1543; Borelli, 1680-1681/1989). In this way, the scientific revolution made it impossible to understand motor control. With a completely passive body, the intelligence of the brain had to be supranatural, and even Newton understood that the control of a mechanical system is not a mechanical problem (Newton, 1704/1952, p. 397; cf. Turnbull, 1959, pp. 367-368). A long sequence of dissidents undertook to ease the task of the brain by revealing the intelligence of the body (cf. Meijer, *in press a*; Meijer, Wagenaar, & Blankendaal, 1988).

In 1663, Robert Boyle wrote that headless butterflies are sometimes capable of procreation, a fact which, apart from the apparent irrationality of procreation, "may be of great concernement in reference to the common doctrine of the necessity of unceasing influence from the brain" (Birch, 1772, p. 71). It took a century before Robert Whytt in Edinburgh would suggest that "the parts may continue to be actuated by the soul . . . for some few minutes after their communication with the brain has been cut off" (Whytt, 1768, p. 291). In Göttingen, Albrecht von Haller was furious: "It is true that Mr Whytt renders the time of death rather shrewdly uncertain. . . . Since, however . . . the soul, when the head has been cut off, loses its empire over the rest of the body . . . it becomes clear . . . that irritability does not depend on the soul" (Südhoff, 1922, p. 14; translation O.G.M.). Neither gentleman was "deficient in irritability" (French, 1969, p. 11), and the row between them was considerable.

Another 100 years elapsed, and Eduard Pflüger published his experiments. When the shoulder of a spinal frog is irritated with acid, the decerebrate animal will scratch it (Pflüger, 1853, pp. 17-18). Remove the scratching leg and the frog will use another leg to rub off the acid (Pflüger, 1853, pp. 124-126). In our present opinion, this result can be used to define spinal cord intelligence: the ability of the spinal organism to find a new solution to a new problem. Rudolph Lotze was abhorred, claiming that physical traces of former experience allow the decapitated animal to mimic intelligence (Lotze, 1853/1891, p. 168)—a sadly improbable hypothesis, since the tail of the headless eel escapes the heat of a flame (Pflüger, 1853, p. 114), and it is unlikely that eels learn to escape fire during the normal course of their life. Clearly, the Pflüger-Lotze controversy (Fearing, 1930/1970) was about the existence and nature of spinal intelligence.

In the Anglosaxon world, spinal intelligence remained more anathema¹⁸ than in the European continent.¹⁹ A 1980 paper from Moscow, written by Fukson,

¹⁸In 1871, Thomas Huxley ran into conflict with archbishop Manning because of Huxley's ungodly reliance on Pflüger's experiments (Huxley, 1870; Manning, 1871). And after Brown (1914) had proposed that the spinal cord contains two oscillating half centers, with mutual inhibition, his name was not to be mentioned ever again in Sherrington's lab. Of course, Sherrington (cf. 1940/1955, p. 217) was a dualist, while in the Soviet Union dualism was not a serious option.

¹⁹E.g., Sechenov, 1863/1965; Verworn, 1907; Bernstein, 1930 (in Beek & Meijer, 1999).

Berkinblit, and Feldman, confirmed Pflüger's experiments in *Science* 127 years after the original publication. Meanwhile, rather spectacular results had been obtained in the group of researchers around Gel'fand and Tsetlin. A decerebrate cat (e.g., Severin, Orlovskii, & Shik, 1967), supported above a treadmill, could be induced to make stepping movements upon electrical stimulation, or with L-dopa, and would adjust its stepping frequency to the speed of the treadmill, even up to trot and gallop. In Moscow society, it was the talk of the day (M.L. Shik, personal communication, 1999). Surprisingly, the KGB failed to recognize spinal intelligence and visited the lab, asking if cats could be prepared to have their locomotion controlled from Moscow Center. They wanted cats as spies, equipped with listening devices, who could innocently enter, say, the White House. The researchers refused to cooperate.²⁰

Internationally, there followed an avalanche of studies on spinal mechanisms involved in rhythmic movement. At first,²¹ it appeared as if such "central pattern generators" (CPGs) were just "music boxes" (e.g., Selverston, 1980), complicated reflex mechanisms responsible for stereotyped actions. Then it was found that the lamprey spinal cord contains mechanoreceptors (Grillner, McClellan, & Perret, 1981), which appeared to invalidate conclusions from all deafferentation studies. Once again, emotions ran high,²² but the CPG-community inexorably drew itself into accepting and studying spinal intelligence. Interest rose for the flexibility of CPGs—through chemical modulation (Harris-Warrick, 1988) or afferent information (Rossignol, Lund, & Drew, 1988); in distributed control (Gelfand, Orlovsky, & Shik, 1988) or coupling between non-linear oscillators (Rand, Cohen, & Holmes, 1988).

To date, there is no doubt the spinal cord can learn (Edgerton et al., 1997b), that is to say, find new solutions to new problems. Spinal cats can be trained to walk independently, the results of training depending on the specific training regimen (Edgerton et al., 1997a). One of us (V.R.E.) trained a spinal cat to stand unassisted on its hindlegs (De Leon et al., 1998). The human spinal cord can interpret load during stepping (Harkema et al., 1977),²³ which appears to be good news for spinal cord patients. It is because of these patients that we don't think that spinal cord intelligence will ever disappear again from the literature.

We can wrap up our tale of two sides of a coin. The dominant image of motor control has been for ages (and in the general populace still is) that the brain dictates the limbs. It took a while to realize that this is impossible (cf. Bernstein, 1935/1967). In our opinion, low dimensional control (as hinted at in the paper on "Tonus") and spinal intelligence (as in the behavior of decerebrate animals) complement each other in solving the conundrum. When Bizzi entered the debate (Bizzi

²⁰[O.G.M.] This story was told to me by four different people, whom I keep anonymous. I particularly want to thank the one who is responsible for the joke on the White House.

²¹For a short historical overview, see Harris-Warrick, 1988.

²²One of us (O.G.M.) wanted to publish on spinal cord intelligence with an otherwise enlightened CPG researcher who, however, refused to even mention the name of Kelso (e.g., 1977) in a scientific paper. A considerable argument ensued.

²³[V.R.E.] We found EMG changes more closely associated with peak load than with tendon-stretch or the velocity thereof. But then, these variables are mutually correlated.

et al., 1982), he came from the opposite direction,²⁴ in search of brain intelligence. Of course, that is perfectly legitimate,²⁵ but it is not what Bernstein and Kots, or Feldman, had been looking for. Then Bizzi found evidence for low-dimensional control and spinal intelligence. Everyone got confused. We have attempted to show that there was confusion all over in the history of spinal intelligence and of low-dimensional control. Just as in marriage (Roth, 1977), when the disagreement goes deep, the arguments tend to be about superficial details.²⁶

Tonus²⁷

N.A. Bernstein and Y.M. Kots

Neuromuscular tone (from Latin "tonus" = tension) is the controlled totality²⁸ of the characteristics of excitability of the neuromuscular apparatus and of the mechanical parameters of the muscle (its resting length, modulus of elasticity, and coefficient of viscosity²⁹). The notion of tone was originally used by Galen³⁰ in relation to mechanisms of postural control. Later, the notion received many conflicting definitions from different authors who related it to different substrates.

²⁴Indeed, Bizzi et al. (1992, p. 606) argue that the "main difference . . . lies in the importance accorded [to] the distinction between feedforward and feedback mechanisms."

²⁵As is the search for spinal mechanisms in the CPG-community (e.g., Orlovsky, Deliagina, & Grillner, 1999).

²⁶Do we "believe" that central control has a positional dimension? Well, movement, as in locomotion, is changing place, so intuitively control in spatial terms sounds attractive. On the other hand, two of us are non-native English speakers, and we would be amazed if our neuromotor systems would be more limited than us. Maybe the neuromotor system is able to speak many languages, depending on individual differences, task constraints, pathology, or strange interventions in the laboratory. But that is beyond the scope of the present paper.

²⁷The paper first appeared in the *Grand Medical Encyclopedia* [Bols'aja Medicinskaja Enciclopedija], edited by A.N. Bakylev, vol. 32, pp. 418-422 & 427. Moscow: State Encyclopedia, 1963. The paper was translated by M.L. Latash and edited for clarity. Footnotes were added by the present editors to clarify particular points or to provide historical context. "[M.L.L.]" indicates a note that was provided by the translator, M.L. Latash.

²⁸A grand opening, a *coup* right in the first sentence. *Tone* is not unconscious or automatic, but controlled. Moreover, *tone* is not just one property of neuromuscular activity (such as the maintaining of posture), but the totality of all relevant properties. Tone was a popular topic in the 1960s, viewed as "the state of readiness of the entire neuromuscular apparatus—the precondition for action" (Pribram, 1971, p. 226), the "canvas . . . on which movement is depicted" (Mettler, 1967, p. 478). In 1966, Bernstein subsumed tone under "the large group of processes, which precede virtually any action and pave the way for it" (Meijer & Bongaardt, 1998, p. 5 & note 14).

²⁹While elasticity is, so to speak, resistance to position, viscosity is resistance to velocity. Since both are apparently controlled, the paper implies that the velocity dependence of the stretch reflex is a controlled property (cf. Feldman, 1986; Feldman & Levin, 1995).

³⁰Galen (2nd century AD) was strongly influenced by Aristotle's theorem that movement presupposes posture, movement being what you do between one posture and another. For Galen's understanding of motor control, see Meijer (in press a).

There are only two phenomena that have always been implied under tone: (a) Mechanisms of postural activity; and (b) slow and steady, low energy contractile processes in muscles—called “tonic” in contrast to forceful, short-lasting “phasic” processes. For a long time, the assumption of the existence of a special tonic type of muscular contraction, assuring the preservation of posture in humans and animals, was supported by studies of invertebrate smooth muscle. It has been established that the processes in the smooth muscles of invertebrates are fully analogous with those in the internal organs of vertebrates. These phylogenetically ancient neuromuscular devices (the paleokinetic system)³¹ are characterized by a number of firmly established features: Neural as well as muscular processes can be graded,³² i.e., they do not obey the “*all or none law*.”³³ Besides, they can be of either positive or negative sign, i.e., they can manifest themselves as either an active excitation accompanied by a contraction or an active inhibition accompanied by muscle lengthening, the signs characterizing corresponding shifts in bioelectrical potential (cathode- and anode-electrotone, *E. Pflüger**). These states of the active muscle are continuous, both in their mechanical and in their electrical characteristics (J. Ewald).

The problem of tone is much more complex when related to the skeletal muscles of vertebrates, in which tonic phenomena are observed simultaneously with phasic contraction processes. Phenomenologically, two types of tone have been identified, the contractile or elastic tone (S. Rieger, E. Spiegel, and others) and the plastic or viscous tone (O. Riesser). In cold-blooded vertebrates, it has been established beyond doubt that there exist two types of specialized elements within the motor apparatus (one participating in the execution of fast, phasic contractions, and the other involved in slow, tonic contractions). Until now, it has been impossible to confirm the existence of a special tonic type of contraction in higher vertebrates and in humans. When tone is discussed as a special type of muscular contraction, one needs to view it in relation to the long-lasting contractions that are generated by smooth muscles.

The main function of the activity of skeletal striated muscle is the generation of a single, phasic contraction, or of a series of such contractions (*Tetanus**). In combination with the characteristic bioelectrical phenomena in the motor nerve and in muscle fibers, this function deserves to be referred to as neokinetic. If we compare neokinetic phenomena with the aforementioned paleokinetic properties of smooth muscle, we see that the regulated changes of all parameters of neokinetic activity in skeletal muscle are identical, in all their features, to paleokinetic processes. Hence, all the phenomena in skeletal muscle that have, at some time, been attributed to muscle tone do not represent a special kind of contractile muscle activity, existing parallel to neokinetic activity, but *the totality of adjustable controls* of the muscle, proceeding according to paleokinetic principles. These adjustments,

³¹*Paleo* (Greek: old) refers to early stages of evolution, and *neo* (Greek: new) to newer stages (from the evolution of birds onwards): Paleokinetics / neokinetics are old / new stages in the evolution of motor control. Starting in the 1940s, Bernstein often used the paleokinetic / neokinetic dichotomy in his papers; cf., e.g., Bernstein, 1945 (in Sporns, Edelman & Meijer, 1998), and Bernstein, 1965 (in Meijer & Bongaardt, 1998).

³²This had been the main point of Bishop's influential 1956 review of the “Natural history of the nerve impulse” (cf. also Pribram, 1971).

³³Items with an asterisk refer to other contributions in the *Grand Medical Encyclopedia*.

that proceed prior to and during the muscle's phasic contractions, define its initial length, elasticity, the compound amplitude of action potentials,³⁴ parameters of the lability and refractoriness of the neuromuscular apparatus, etc. At the present time, the characteristics of the activity of skeletal muscle at rest and during postural activity should not be viewed as displays of a special type of muscle contraction, but as correlates of the regulation of this activity.

Now, the reflex regulated nature of tone is beyond doubt. The existence of so-called "reflex tone" is supported, in particular, by the dramatic drop in the muscle tonic contraction after its deafferentation. A role of higher brain centers in the control of tone has been established in animal experiments. In particular, a transection of the brain stem at the level of the rubral nuclei induced the typical picture of decerebrate rigidity (see *Decerebration**) with a parallel increase in the tonic vestibular and collico-tonic trunk reflexes (see *Reflexes of Magnus-De Klein**). The main reflex mechanism of tone—the stretch reflex or the myotatic reflex (E. Liddell, C. Sherrington)—was originally discovered and studied in rigid extensor muscles of decerebrate animals. To date, it has been established that the stretch reflex involves a number of reflex loops (R. Granit) that assure the self-regulating adaptation of reflex tension³⁵ to muscle length (the stretch reflex system).

For a long time, the decerebrate "model" of tonic reflex mechanisms formed the basis to understand the normal regulation of long-lasting contractions of resting and postural muscles in the healthy human. However, direct human studies of muscle biopotentials have shown that neither in the state of rest nor during postural activity do human muscles behave according to this model.³⁶ Central regulation does not become manifest in a continuous reflex contraction of muscles but in reactions that occur in response to changes in a muscle's length. In particular, this assures continuous corrections of disturbances of the vertical posture during up-right standing (V. Gurfinkel).

Figure 1 illustrates in a schematic way the segmental mechanisms of the stretch reflex. Stretching an extensor muscle brings about a volley of impulses in the fastest conducting afferent fibers (Ia) that originate from the primary endings (nuclear bag) of a muscle spindle (ms). These fibers make monosynaptic connections on the motoneuron of the extensor muscle (M_{α}) and induce its reflex discharge (classic stretch reflex). Muscle stretch is also an adequate stimulus for afferent endings in the Golgi tendon receptors (G); however, their threshold of excitation is somewhat higher than that of the primary spindle endings. Impulses from the excited tendon receptors also travel very fast along conducting fibers (Ib), but they are interrupted by an interneuron (B_1) on their way to the motoneuron that innervates the stretched extensor muscle. Signals from the tendon receptor exert inhibitory effects on the motoneuron, but these effects are delayed as compared to

³⁴At the time, electromyography could only reveal total electrical activity. Note that the formulation in the paper is unfortunate, since EMG-activity is an emergent property once the other parameters have been set (Feldman, 1986; Latash, 1993; Feldman & Levin, 1995).

³⁵[M.L.L.] In the original, an ambiguous term is used that can mean either *force* or *strain*. Therefore, an equally ambiguous term, *tension*, is used in the translation.

³⁶There is an interesting analogy here with rejecting the argument that spasticity in stroke would "prove" that the brain is needed to specify the details of normal movement. In fact, the stroke patient is not trying to move without a brain; to the contrary, the stroke patient has to move with a deranged brain.

Figure 1 — Segmental mechanisms of the stretch reflex. Note: m = muscle fiber; ms = muscle spindle; G = Golgi tendon receptor; Ia = afferent fiber from a primary spindle ending; II = afferent fiber from a secondary spindle ending; Ib = afferent fiber from the Golgi tendon receptor; α = large efferent (motor) fiber; γ = small efferent (gamma) fiber; M_α = large motoneuron; M_γ = small (gamma) motoneuron; B , B_I , B_{II} = interneurons.

Figure 2 — A "length-tension" diagram.

the excitatory effects from the primary spindle ending because of the higher threshold and the synaptic delay. The inhibitory effects are furthermore increased by the reflex muscle contraction which is an adequate stimulus for the tendon receptors. Extensor motoneurons are also inhibited by impulses from the secondary endings (myotubes) of the muscle spindle.³⁷ These receptors likewise have a higher threshold to stretch as compared to the primary endings of the muscle spindle. Their afferent effects are mediated by a slowly conducting group of fibers (II) and are interrupted within the spinal cord by at least one interneuron (BII). Hence, a stretch of an extensor muscle first involves the stretch reflex which is later reduced or completely inhibited by delayed inhibitory effects from the tendon receptors and secondary endings of the muscle spindle (inverted stretch reflex). The quantitative relation among the excitatory and inhibitory effects defines a linear relation between reflex tension and muscle length (P. Matthews, R. Granit).³⁸

On a "length-tension" diagram (Figure 2), this relation is expressed as a segment of a straight line whose leftmost point (A) denotes the threshold of the stretch reflex, the rightmost point (B) the threshold of the "lengthening reaction,"³⁹ and the slope with respect to the abscissa (α) the magnitude of the reflex reaction.⁴⁰ These three parameters characterize the degree of activity of the stretch reflex. They are controlled by suprasegmental influences that define the quantitative balance of excitatory and inhibitory afferent influences on the common final pathway (shown in Figure 1 as the extensor motoneuron). An increase in the activity level of gamma-motoneurons (M_γ), that innervate intrafusal contractile fibers of the muscle spindle, produces an increase in the excitatory effects on the motoneuron. Contraction of the polar zones of a muscle spindle leads to an increase in the sensitivity of primary endings to stretch, thus increasing their excitatory effect on the motoneuron. Hence, suprasegmental centers act on gamma-motoneurons and define the magnitude of the afferent excitatory inflow by controlling the threshold (the leftmost point of the straight line) and the magnitude (the slope of the line) of the reflex reaction.⁴¹ The most specific effects on the gamma-motoneurons are produced by the *reticular formation** which is the primary mediator of the influences of other afferent systems (such as vestibular and visual analyzers, and others) on the stretch reflex. An increase in the excitatory effects from contracting muscle fibers is accompanied by a parallel increase in the firing of secondary

³⁷See the note by M.L.L. in the next paragraph.

³⁸Note that such a physiological length tension diagram is different in principle from Feldman's "invariant characteristics," which capture how the system finds an equilibrium-point for any given value of lambda in the presence of an external load (cf. Asatryan & Fel'dman, 1965; Fel'dman, 1966a).

³⁹These first two parameters form Feldman's (e.g., 1986) range of lambda, which in healthy subjects is larger than the actual range of motion, whereas in stroke patients it may be the factor that limits motion (Levin et al., 2000).

⁴⁰At the level of the joint, slope plays a central role in Bizzi's equilibrium-point hypothesis (Bizzi et al., 1982 & 1992). In Feldman's lambda model, it is the C command that (co)determines slope (e.g., Feldman & Levin, 1995).

⁴¹It is in particular this statement and the way it is worked out later in this paragraph which, in our present understanding, allows for an interpretation of the paper on "Tonus" in terms of low-dimensional control.

endings⁴² that exert opposite (inhibitory) effects on the motoneuron. However, this inhibitory "shadow" is also controlled by suprasegmental (and segmental) influences directed at interneurons that mediate the effects of the secondary endings on the motoneuron. There is a similar type of control of the magnitude of the inhibitory effects from the tendon receptor on the motoneuron. Thus, suprasegmental centers define the magnitude of the excitatory "input" in a direct way (via the gamma-system) and of the inhibitory "input" in an indirect way, i.e., by acting on interneurons. If the excitatory "input" is unchanged, the inhibitory "input" defines the magnitude of the reflex reaction (the slope of the straight line) and a muscle length at which the stretch reflex is inhibited (the threshold of the "reaction to stretch"—the rightmost point of the line). Noteworthy, "tonic" effects from suprasegmental centers are not mediated by direct influences on the motoneuron (the final pathway) but by the regulation of the afferent "input" that defines the characteristics of muscle work during its reflex activation as it originates from stretch.

Therefore, the notion of tone should include both the aforementioned paleokinetic mode of muscle regulation and a neokinetic form of regulation. In this sense, tone becomes the main adaptive function of the skeleto-motor apparatus which tunes its current state and the excitability of its structural parts to tasks of active postural or movement control in accordance with afferent signals from all types of receptors.

Different methods of tone assessment and measurement in humans may be classified into "direct" and "indirect". Indirect methods include measurement of secondary phenomena that can accompany changes in tone: 1). Measurement of cross-section muscle hardness—sclerometry; and 2). Measurement of intramuscular pressure as muscle tissue resistance to an intramuscular injection of a physiological solution. Direct methods of tone assessment are based on measurement of muscle passive resistance to its longitudinal stretch. Among these methods, equitonometry produces the most accurate results. This method does not allow to characterize the tone of a single muscle but the tonic balance of antagonists acting at a given joint with respect to a motion when the effect of gravity on the moving segment is eliminated.⁴³

⁴²[M.L.L.] This description is outdated (e.g., Rothwell, 1994). Secondary endings show a drop in their activity during an active muscle contraction, accompanied by shortening of the extrafusal muscle fibers. Their inhibitory effects on extensor motoneurons are mediated by interneurons in the flexor reflex loop. Note that Bernstein and Kots describe only effects of secondary endings on extensor motoneurons. If they considered a flexor muscle, the sign of the effects from secondary spindle endings would change, and the seemingly noncontroversial and elegant scheme of reflex connections (Figure 1) would require a major overhaul.

⁴³Thus ends a strangely fascinating paper, written in an encyclopedia, which may have ensured that the paper was never cited again. Of course, the ideas presented did not come as a bolt from the blue, as Merton (1953), Granit (e.g., 1955) and, for instance, Matthews (e.g., 1958a & 1958b) had worked on similar conceptions. Nor did the debate on low-dimensional control come to an end, as many (e.g., Asatryan & Feldman, 1965; Feldman, 1966a & 1966b; Gurfinkel et al., 1966; Bizzi et al., 1982; Feldman, 1986; Bizzi et al., 1992; Latash, 1993; Feldman & Levin, 1995; Feldman et al., 1998) undertook to travel further in the same direction. Still, there is a lesson to be learned from the 1963 paper on "Tonus." The ideas were still sufficiently vague to avoid conflict over details. On the other end, some aspects were still so new that even the authors themselves did not fully understand. And so it should be.

Epilogue: "No big deal"

Since very little is known about the background of the paper on "Tonus," we decided to include a conversation between Onno Meijer (M) and Yakov Kots (K), which took place on the 11 September 2000, at Kots's Sherman Oaks home (Los Angeles), followed by a superb dinner with the three of us.

M: It took me some time to locate you. I finally got your telephone number at "Progress in Motor Control II," August 1999, Pennsylvania State University. Weren't you surprised when I called?

K: Well, I proudly told my granddaughter that a man was coming from Amsterdam to talk about a paper that appeared 37 years ago.

M: If one reads the paper, it becomes clear that it has two different parts. You obviously are the main author of the part that starts with Figure 1. Could you give us some background as to yourself?

K: I was born in Moscow in 1931. My father was an economist, my mother a physician. During the war, my father was killed at the front, and when Hitler approached Moscow, we moved to Soviet Asia. After the war, I was hungry every day; the first time I was full again was in 1947. My mother passed away in 1948, and I lived with my twin sister without any financial support. I studied radio-electronics for one year, but then switched to medicine, probably in honor of my mother. In 1955, I got my degree from the First Moscow Medical University and started to work as a sports physician, which was my field of interest. I then entered the Institute of Child Physiology and started to work with Farfel to prepare for my first dissertation.

M: That is where "equitonometry" comes in, isn't it?

K: Yes. It means equi-tono-metry, that is, measuring if the tone is the same on two sides. I still don't know who invented it. Maybe Farfel, maybe Bernstein himself. You have to imagine two tables in series, so that a person can lay on them with his head on the proximal table and his feet on the distal one. A small space is left open between the tables so that the proximal one (the "plateau") can rotate around a vertical axis. The plateau has only one leg, which is in the middle of the side adjacent to the distal table. At the beginning of the experiment, the connection is locked, and when it is unlocked, friction is very low so that even small asymmetries will lead to rotations of the plateau.

In cases of tonic unbalance, the plateau will rotate to the side with the highest tone. Supine children with scoliosis show a clear asymmetry in tone. We attached a weight (via a pulley) to the plateau and then removed it, studying the effects on the rotation of the plateau. I also studied head movements and had test persons lie on their side. Inspired by Floyd and Silver, I analyzed the tonic balance between muscles of the back and the abdomen, and their reactions to stretching in different conditions. When test persons on their side are fully stretched, the plateau moves forward because of tonic activity of the abdominal muscles. There is balance when the angle between the upper leg and the trunk is 120° , that is, when you either bend your trunk forward or flex your upper leg by 60° .

M: On the television, I am just seeing some astronauts in the space shuttle. The angle between their upper leg and trunk is 120° . Is that what you discovered?

K: Sure. So, because of these experiments, and reading Granit and Matthews, it was quite natural to think that the threshold and the slope of the stretch reflex are controlled.

M: Is that how Bernstein heard of your work?

K: Farfel must have told him, and Bernstein was immediately enthusiastic, probably because he didn't believe that force control could have stable results, and this seemed a plausible alternative. He invited me to co-author the paper on "Tonus," and I visited him at his home many mornings (while in the afternoons he would be on morphine). For me, Bernstein was like a god. I was so proud when he praised my work, and when he said that he would be an official opponent for the defense of my first dissertation (1961). Still, to the best of my knowledge, he never read Granit or Matthews. He just wasn't as interested in the details as I was. He liked grand principles and wanted to talk about them.

M: Do you know that after your paper with Bernstein, he never referred to stretch reflex control again? Instead, he began writing of segmental "transformation matrices" [cf. Bongaardt, Pickenhain, & Meijer, 2000; Latash, Latash, & Meijer, 1999, 2000], that are under control of the higher centers, but once the parameters are set they follow their own rules.

K: I didn't know that, but I don't blame him at all. We remained very close; at the end, I was even responsible for the organization of his funeral. In fact, I also changed my research topic. I joined Gel'fand's biophysics lab and felt that I had closed the mechanical part of my work. I wanted to enter neurophysiology and studied what happened to the H-reflex in preparing for a movement. This would become my second dissertation, eventually published in English (Kots, 1977) with the help of Edward Evarts, the famous neurophysiologist.

M: What were your experiences in the Gel'fand lab?

K: I found the atmosphere in the Gel'fand lab very stimulating, and I was fond of many people working there. Particularly Tsetlin was very inspiring. But then, in the Soviet Union you never knew whose name would appear on top of your own paper (I don't mean Gel'fand or Tsetlin). Because of that problem, I wanted to create my own niche. Friends knew of my problem, and in 1965 I could get a job in the training of astronauts, or one in the Central Institute of Physical Culture. I opted for the latter because I thought it would be less political.

M: But you are well aware that sports in the Soviet Union was a very political affair.

K: Yes, of course. I developed equipment for muscle stimulation, which could be used medically (for example, in scoliosis treatment), and also in the training of athletes. The effects were astounding. So, there came an official agreement between the governments of the Soviet Union and the German Democratic Republic, where they would get my muscle stimulation and we would get access to their doping program. I had little to do with all that, and there were also very positive aspects of my engagement in sports. I met, for instance, with Lothar Pickenhain [cf. Bongaardt, Pickenhain, & Meijer, 2000] who at first seemed to be a rather daunting official, but soon we became close friends. And then there was traveling abroad. I was physician of our top athletes and went several times with them to other countries. Of course, that was never easy, because the authorities would instruct

you on how to behave and would precisely follow whatever you did. There was that story of a Russian official who went to Finland and commented: "What a delicious milk!" He was never allowed to go abroad again because he had offended Soviet agriculture.

M: Was that the reason you wanted to leave?

K: Yes and no. For a long time, my life in the Soviet Union was depressing; I had physical and personal problems. When I recovered, I realized that I couldn't bear the lack of freedom any longer. And there was no impetus for the people to work in the Soviet Union. Such a system can never survive.

M: Were you happy when you arrived in the West?

K: The first thing I discovered was that some people had stolen my idea of muscle stimulation. They heard about it when I lectured on medical applications in Montreal; they patented it and became rich. When I finally arrived in the West to live here, I found out that I was already famous. I read in a book that I hadn't known before: "Who is this Dr. Yakov M. Kots? . . . He is, in short, one of the modern giants of sports medical research and the developer of Stimul One, the most amazing development in the field of electric muscle stimulation in three decades, a machine that one day might revolutionize the treatment of back and muscle injuries all over the world" [Gilbert, 1980, pp. 175-176]. That is certainly praising language, but I never saw any of the money that came out of the patent.

For a while, I worked with doctor Cley in the Chiropractic Rehabilitation Center in Saint Louis. Then, I did scientific work with Reggie Edgerton, here in Los Angeles, until I retired. Do I like it? I am not rich, but people respect me, and I really enjoy that feeling of freedom. Even when you drive a car, people are polite, they give you space. Still, you always remain an immigrant. My English is not very good, and that is a major handicap here.

M: Back to the paper. You know that I liked it very much when I read it, and so did Mark Latash.

K: At the time, I was happy with Bernstein's compliments, and I was excited about the paper. But it followed logically from Granit and Matthews, and from my own work on equitonometry. Actually, I think it was no big deal. So, in a way, the story of "Tonus" is the story of my life.

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⁴⁴There are two mysterious "B."s and one mysterious "P." in these references. Maybe the "P." is a typing error, and the symbols just refer to "Bibliography."

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