Bernstein's Dynamic View of the Brain: The Current Problems of Modern Neurophysiology (1945)

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with endnotes provided by Onno G. Meijer

In 1945, in a country devastated by the second World War, N.A. Bernstein addressed the Joint Conference of the Societies of Physiology and Neuropathology and delivered a paper titled "The Current Problems of Modern Neurophysiology." This paper was subsequently published in the *Physiological Journal of the USSR*. It is reprinted in this issue of *Motor Control*, translated into English for the first time. Bernstein presents a concise account of the neurophysiology of his day, at the same time sketching out several theoretical notions on the operation of the nervous system. The article links considerations of the dynamics of movement (the overt manifestations of brain activity) to the processes and mechanisms of brain function. From a present-day perspective, Bernstein's outlook on contemporary neurophysiology was a thoroughly modern one, with brain function rooted in the evolution of morphology and behavior, dominated by the action of large populations of neurons acting as collectives, and regulated by modulatory systems.

From the outset, Bernstein placed the scientific study of the brain in the context of evolution ("phylogenesis") and stressed the central role of the relationship between body and brain morphology. He emphasized the important role of behavior ("effector function") in the survival and evolutionary success of organisms. He viewed the evolution of "receptor functions" (sensory systems) as intricately linked to that of effectors, mainly through their role in planning motor actions and relaying the sensory consequences of movement. The notion that nervous system structures, during evolution (its hallmark being progressive "encephalization"), undergo significant functional changes ("switches") is clearly expressed. As in most of his writings, Bernstein criticized orthodox Pavlovian reflexology, in particular toward the concept that behavior (motor function) results primarily from the activation of reflex arcs, organized as sequential chains linking sensory stimuli to stereotypical motor acts. Instead, behavior is a means by which organisms autonomously act upon their environment. The decidedly anti-

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Pavlovian bent of his theoretical framework contributed to Bernstein's political difficulties in the early 1950s.

Bernstein noted the substantial progress in electrophysiology taking place in his day ("Contemporary amplifiers have literally allowed to see the invisible," he wrote). Most interesting is his discussion of the relationship between single neuron discharge and the population signal recorded by electroencephalography, a method developed some years earlier. He correctly perceived that the very fact that large surface potentials can be recorded points to dynamic interactions between cortical oscillators that "attract one another into large constellations demonstrating a single frequency." He presented a simple mathematical argument for the existence of frequency- and phase-locked oscillations between individual cortical cells. Assuming statistical independence between a set of $2n$ binary units, he showed that, on average, the overwhelming majority of units cancel each other out. In other words, the number of system states with an equal or almost equal number of ones and zeros is overwhelming, if the units do not interact. However, given the relatively large signals obtained by electroencephalography, he concluded that "there has to be an inevitable synchronization, both by frequency and by phase, of numerous low-frequency oscillators in the cortex."

From today's point of view, this conclusion is astonishingly modern. Since the late 1980s, the concept of synchrony and temporal correlation as key ingredients of cortical function has become a focus of attention in neurophysiology (e.g., Singer & Gray, 1995) and computational modeling (e.g., Sporns, Tononi, & Edelman, 1991). Bernstein's remarks foreshadow this significant development. They also show that Bernstein's conception of biological systems as coherent entities made up of interacting parts was not limited to the study of movement (the "extrinsic dynamics"), but that his thinking extended to the firing patterns of nervous systems (the "intrinsic dynamics") as well. Bernstein's brilliant grasp of the principles of self-regulatory systems (anticipating, as pointed out by Luria, 1967, the development of cybernetics by a number of years) is again evident. However, Bernstein did not submit to strict determinism. In his view spelled out in this article, cortical neuronal operations incorporate significant elements of stochasticity, yielding variable patterns of neural and motor activity. Thus, the synergy as a basic unit of motor coordination (a concept developed further by Gel'fand and colleagues; see, for example, Gel'fand, Gurfinkel, Tsetlin, & Shik, 1971) finds a neural counterpart in variable and dynamic cell "constellations" (anticipating the rather more deterministic cell "assemblies" of Hebb, 1949, and Hayek, 1952). Just as behavior is not the stereotypical outcome of reflex action but an autonomous act of intervention upon an environment, the firing of neurons is as much the result of input stimuli as of neuronal coordination. Although Bernstein himself did not think in these terms, it has been noted earlier that his views were quite compatible with theories of brain function based on reentrantly interacting neuronal groups subject to variation and selection (Edelman, 1987). Inspired by Bernstein's theories, we have proposed that an organism's ability to master multiple redundant degrees of freedom can be explained by the generation of variable motor patterns and their subsequent selection by differential amplification (Sporns & Edelman, 1993).

Bernstein discusssed how fast cortical activity (the "neokinetic telegraph spike process") is modulated by the slower activity of evolutionary ancient ("paleokinetic") autonomic systems. He distinguished "post factum" secondary adjustments and "ante factum" anticipatory settings. Again, Bernstein correctly

identified a highly significant area of neurophysiology, one that through the intensive physiological and pharmacological studies of diffuse modulatory systems of the brain remains of central importance today. Perhaps with some irony, Bernstein referred to the interplay between paleo- and neokinetic processes: Autonomic processes, while ancient, continue to act as regulators for the powerful but "blind" neokinetic discharge patterns, consisting of spikes that are limited in terms of spatial effects, temporal duration, and information content. While Bernstein's arguments are partly obscured by an arcane terminology, his basic distinctions remain of interest today.

Bernstein's achievements and insights are all the more remarkable if one considers his relative isolation from mainstream European science, the upheavals and devastation of the second World War, and the perilous intellectual climate of Stalinist Russia, conditions he endured for most of his working life. Bernstein's influence greatly increased with the translation and publication of *The Coordination and Regulation of Movements* by Pergamon Press in 1967, shortly after his death in 1966. Several modern approaches to motor and cognitive development, from dynamic theories of motor coordination (Kelso, 1995; Thelen & Smith, 1994) to very recent concepts of "embodied cognition" (Clark, 1996), were influenced, directly or indirectly, by Bernstein's thought. The present article shows that Bernstein's theories were not limited to the realm of motor coordination but were coupled to an emerging understanding of variability and stochasticity in brain function.

The Current Problems
of Modern Neurophysiology[1,2]

N.A. Bernstein

1. A genetic study of the excitatory and reactive systems of animal organisms has shown that the succession of leading links in the development of nervous and kinetic systems is the most important evolutionary principle with respect to structures as well as functions. No true understanding of the structure and functions of the neurokinetic apparatus in humans is possible if this most decisive factor is overlooked.

2. With respect to both structure and function, the central nervous system of the *Vertebrata* reveals the closest synthetical unity between the earliest and the most recent (the paleo- and the neokinetic) of structural and functional principles, which are manifest in all the regions of the central nervous system (both in the cerebrum and in the spinal cord) and in the neuromuscular periphery as well.

3. One very characteristic and general feature of this unity should especially be noted, that is, the mainly executive role of neokinetism and the adaptive regulatory role of paleokinetism, which are confirmed by numerous examples.

4. Studying the two characteristic classes of central nervous regulations observed (i.e., the preliminary or "adaptive"[3] and the secondary or corrective regulations) sets forth the following three essential problems of present-day neurophysiology: muscular tonus, inhibition, and active rest. At present these three notions are of a heterogeneous nature and demand a detailed classification of far greater exactness.

5. The most urgent task of neurophysiology is to study the genesis and struc-
ture of the adaptive and regulating processes—under both normal and patho-
logical conditions—that manifest themselves in the complex synthetic effects
of physiological tonus, central inhibition, and active neuromuscular rest. A
genetic approach to analyzing these physiological categories with the help of
up-to-date experimental techniques will make it possible to reveal the most
general, pressing, and important neurophysiological regularities.

Now,[4] when physiologists and neuropathologists are celebrating the anni-
versary[5] of the idea of reflex[6] and paying homage to its founder, Descartes, and to
the great Russian scientists Sechenov[7] and Pavlov,[8] who advanced the science of
reflexes, it appears reasonable to attempt a prognosis for the theory of reflexes
based on the contemporary situation. One needs to start by summarizing what is
essentially new in contemporary science as compared to the times of Sechenov
and Pavlov.

Contemporary natural science invariably starts with the principles of
phylogenesis and morphogenesis in any physiological study or any attempt to ex-
plain experimental facts. The former principle originates from the desire to con-
sider phenomena in their development,[9] while the latter stems from accepting the
necessity of a mutual correspondence between structure and function.

Evolution of the Brain[10]

The evolution of the central nervous system of vertebrates is characterized not by
a principle of expansion but rather by a principle of addition of qualitatively new
formations that had no homologous counterparts in the nervous systems of more
ancient life forms.[11]

This principle leads to inevitable qualitative jumps in the development of
the central nervous system, because of the discreteness of neural schemes: Complica-
tion of a reflex arc or any other route of a neural impulse within the central nervous
system can occur only by involvement of an integer number of new interneurons. The
route along which the central nervous system follows these jumps can be revealed by
such episodes as, for example, the development of the optical apparatus from am-
phibia to birds, with its transfer from a single neuron scheme, "retina–tegmental nu-
clei," to a two-neuron scheme, "retina–external geniculate body–visual cortex."

For a certain amount of time, both apparatuses, the old and the new, function
in parallel. Then, either involution of the old apparatus occurs, as happened in the
mesencephalic visual nuclei, or, more frequently, the old apparatus is modified to
form a more complex synthesis with the newer one. This happened during the
continuous[12] development of the effector systems in the brain. This is how, step by
step, a structure is built, based on the collaboration of several neural levels.

It is necessary to emphasize, however, that the neuronal construction prin-
ciple of the nervous system itself was not born in one step and was not always a
satellite[13] of the evolution of the central nervous system. The nervous systems in
praevertebrata are not neuron-based. Even in vertebrates, up to the highest mam-
mals, the construction of the postganglionic part of the autonomous nervous sys-
tem is closer to that of the neuropile[14] rather than to the neuronal scheme. The
central nervous system of vertebrates works with the neuronal principle for some
classes of function, and, at the same time, as a continuous, diffuse neuropile for
other classes of function.

Not a single original structure of the nervous system remains unchanged during the whole process of evolution; this is not only true for the neuronal principle. The evolution of the central nervous system and its continuous structural complications were always dictated by the complications of the biological problems the species had to solve. In the course of phylogenetic history, there is a slow change in the leading element[15] that defines the progress and direction of the evolution of the central nervous system.

At the early stages of phylogenesis, such a leading element was, without doubt, the effector function: The fate of an individual in the evolutionary struggle is crucially dependent on its actions and on the higher or lower adequacy of its reactions to the external world. Receptor functions served the effector function both as signal systems (here, the emergence of telereceptors was particularly important) and as systems that ensured sensory corrections, necessary for successful motor coordination. The emergence and refinement of telereceptors were directly defined by the biological necessity of locomotor, integral movements of the whole body, which represented the next developmental step against the background of ancient, metameric motor reactions that could be satisfactorily served by tangoreceptors.

After the priority of telereceptors was established, these receptors took the leading role in evolution. In their turn, according to Sherrington's generalization, they defined the further process of centralization of the nervous system and the intensive development of neural ganglia at its rostral end. Thus, another shift of the leading level occurred at evolutionary stages that are closer to our own times, following events which allowed Sherrington to say that "telereceptors created the brain." From a certain point in time, head ganglia, which integrated information and served telereceptors, turned into the dominating organ that took sole control over the subsequent route of development. The domination of the central nervous system during the current state of the evolution is beyond doubt,[16] not only determining external functions but also autonomous functions such as trophics, metabolism, and the immune system.

The next complication, emphasized by all researchers starting from Monakow and Economou, is the encephalization of functions[17] that modified the most important workings of the nervous system and changed their interrelations and significance. Functional encephalization can be directly related to the above-mentioned slowly progressing domination of the brain. This steady process of encephalization (also called "progressive cerebration," "corticalization," etc.) has led to qualitative changes in even the most ancient functions of the nervous system, switching them to new, differently organized substrates.[18] In relation to the growing recognition of encephalization and its importance to brain science, it is interesting to point to the shift in the preferred species of experimental animals during the last century: Sechenov, Flourence—frogs and doves; Sherrington—cats; Goltz, Pavlov—dogs; Bechterev, Leyton, Grünbaum—rhesus monkeys; contemporary American scientists and Pavlov (the latest works)—apes; neurophysiology of the World Wars—human beings.

Paleokinetic and Neokinetic Phenomena

The role of clinical neurology[19] in the development of brain science during the last hundred years, in particular during the 20th century, does not need to be emphasized. It is sufficient to name Monakow, Wilson, Economou, Förster, husband and wife Vogt, Kleist, Goldstein, Gurevich, Luria, and many others, and to recollect

the clinical material that provided for the understanding of the extrapyramidal system, cortical localization, and neural trophics.

Earlier, it was commonly thought that a physiologist–vivisectionist who worked with animals had huge advantages over the human physiologist, who was limited by the clinical material that was supplied; now this view needs to be reconsidered. The enormous traumatic material of the current war supplied clinicians with such unique natural experiments as would have never been invented even by the brightest imagination of a vivisectionist.[A]

In the area of instrumental and measuring technology, in particular electrophysiology, we can now witness progress which is even more substantial than that in the structural physiology of the nervous system. The last 60 to 80 years have provided physiologists with milliseconds and microvolts (millimicrons of distance were well within reach during the 19th century).

Contemporary amplifiers have literally allowed us to see the invisible during excitation of an isolated excitable element. Physiologists of the 1860s viewed an "action current" in a muscle merely as a short-lasting interruption of what was labeled the "steady-state current," a fleeting violation of the routine. In between individual "spikes"—as they were recorded by a capillary electrometer or a spring galvanometer, constrained, as in a rigid frame, by latency and refractoriness— were intervals of inactivity, of rest, which only allowed for the a priori philosophical compulsion to search for processes of assimilation and resynthesis, concealed from the observer. Needless to say, much more interesting than the spikes themselves were the pauses of "rest" when the electronic tube for the first time announced their intense microvolt content.

Contemporary physiology is characterized by a growing attention to the motor states of the organism,[20] such as labor, sports, and so forth, as compared to the states of basic rest that were predominantly studied in earlier times. Action turned out to be more informative than rest. On the other hand, the so-called "rest," which forms the background and the basis for action, was unexpectedly rich in its physiological significance since it started to reveal to the inquisitive observer an inexhaustible number of prerequisites for action, such as primings, intentions, routings, and preimpulse commutations ("aiguillages"[21] of Lapicque).

All three levels of the somatic nervous system—the peripheral neural net, the spinal cord, and the brain—revealed, to different observers and in different experimental appearances, dual chains of phenomena that can be now identified.

Phenomena of the first type, which can be seen in all three aforementioned substrates, are electronegative spikes whose amplitude is of the order of a millivolt, with a small notch. They were unambiguously identified in the electroencephalogram with the β-frequency range (Berger). These spikes, with their neverfailing tendency to proceed in series, receptor volleys, and effector tetanic discharges, were the first to be noticed among all the action electrophysiological phenomena. They are always characterized by a short duration, reflecting their very unstable states, an omnipresent electronegativity (there are absolutely no "spike positrons"), and a phase wave of fast, bidirectional conduction along fibrillary substrates. Besides that, they obey the all-or-nothing law, show refractoriness following each discharge, end with a complex, multiphasic postexcitatory "tail," and display clear and abrupt strength and speed thresholds of excitation. In order to keep the text that follows clear, let us unite the mentioned phenomena into the neokinetic group, thus reflecting its relative phylogenetic youth. The neokinetic principle of excitation

emerged simultaneously with the rigid, multijoint skeleton, the striated muscle, the myelinated axon, and, possibly, the neuronal structure of nervous systems.

The second form (let us, for the time being, address it as a "microvolt" form to justify its later discovery[22]) is extremely multifaceted. In a peripheral neuron, it primarily reveals itself in the phenomena of trace potentials, with an unambiguous parallelism and a precise synchronization between, on the one hand, electrotonically shifted potentials, and, on the other hand, simultaneous shifts of all the characteristics of excitability and the parameters of excitation. The same group of phenomena involves all types of electrotonic shifts of excitability and conductivity, of any genesis, and, in particular, alternating shifts of both signs of a potential (toward catelectrotone as well as anelectrotone), united under the terms "parabiosis" and "antiparabiosis" in the works of Vvedenski and Vasilyev (1941).

All the phenomena of this microvolt group (representing traces of a discharge of neokinetic excitation, or brought about by another cause) are characterized by very close relations to two types of events that have been well studied in different substrates: excitatory–inhibitory processes in the diffuse nervous systems of lower invertebrates, and phenomena that are typical of the neural processes within the peripheral parts of the autonomous system in vertebrates. These close relations allow us to characterize the whole group as paleokinetic.

Processes characteristic of this group are biphasic; the antithesis of their inherent polar states has been addressed in physiology, depending on conditions of their detection, with many pairs of terms: excitation and inhibition, catelectrotone and anelectrotone, superficial and deep parabiosis, effects of sympatins E and I, and so forth. States with both signs are graded (they do not obey the all-or-nothing law), equistable, and equiprobable. These states do not have clear thresholds, they can irradiate, they require long-term preparation ("beating the trail," "facilitation"), and they lead to a gradually decrementing residual discharge ("after-discharge"). It is of particular interest that we can recognize in paleokinetic phenomena all the details of the neural processes of autonomous and invertebrate nervous systems, transplanted onto new soil. Not only in myelinated axons but also in the skeletal muscle, the same phenomena are associated with mechanical events which precisely copy the processes that are typical of smooth muscle tissue, internal or invertebrate.

It is impossible to find a better definition for mechanical phenomena typical of skeletal muscle tone[23] than to address them as the paleokinetic mode of muscle work. Similar to all processes within the paleokinetic group, muscle tone is biphasic; it possesses not only active contraction but also active relaxation, accompanied by anelectrotonic shifts of the observed potential, for example, during the reciprocal blockade of antagonists.

The most important feature of the paleokinetic group is its humoral nature, its very tight and multifaceted relation to chemistry. Mediators were originally discovered in autonomous systems and are inseparable from paleokinetic processes in somatic systems. The deep relation between postexcitatory trace processes and metabolism was originally emphasized by Ukhtomsky. The relation of trace electrotonic shifts to the resynthesis of unstable chemical chains exploding at the time of a neokinetic spike, and the overlap of these shifts in a ganglionic cell with the flat part of a tooth in a tetanic relaxation "saw" (i.e., with the phase of accumulation), are beyond doubt.

It is quite possible that the neokinetic process emerged from these ancient humoral ones. The bioelectric component against this humoral, chemical back-

ground, typical of the humoral process, separated at some point from the humoral process and gained basic importance as a fast and powerful telegraph signal. In turn, the chemical component turned into a satellite, a metabolic "tail," following the electrical phase wave on the ion–colloid[24] substrate. This switching of roles exemplifies one more case of evolutionary change of the leading element. Further, we will see the immense regulatory importance of this seemingly subordinate, ancient neurohumoral process in neokinetic neural apparatuses and systems.[25]

Paleokinetic Phenomena in the Spinal Cord

Since the discovery of the method of recording cortical electroencephalograms, through a simple trepanation opening or even from an undamaged scalp, the spinal cord has become the least accessible part of the nervous system for physiological observations. Our guesses about its functions and processes can only be based on indirect evidence. A number of phenomena within spinal physiology, however, can be classified with certainty as related to the paleokinetic cycle.

First are the "central excitatory state" and "central inhibitory state," Sherrington's CES and CIS; even that author himself was undecided until very recently whether to consider them as belonging to the biophysical[26] or humoral class of phenomena. Further, low-voltage shifts of biological potentials ("slow potentials") that display slow, irregular curves were explicitly classified by Fulton (1943) as members of the class of electrotonic changes. Also included are numerous types of selective, specific inhibitions and blocks at synapses on ventral horn cells: events of subordinating (electrotonic) control of iso- and heterochronism of the final neuron, and events of reciprocal inhibition of antagonist muscles and contralateral-crossed muscles during alternating stepping-like movements (stepping reflex). Processes of the group of Sechenov inhibitions,[27] for which transmission through the autonomic system (i.e., by an unarguably paleokinetic route) has been firmly established, are also included.

Finally, there are numerous events in spinal synapses that behave as paleokinetic islands inside a huge neokinetic machine with their inherent iterative nature (Lapicque's term, which is nearly synonymous with our "paleokinetic"), synaptic delays directly related to the transformation of an electrical process into a humoral one during the short-lasting instant of stepping over the synaptic cleft, with their routing, dendritic irradiation, after-discharge, and so forth. These are unlikely to represent different phenomena only because they were observed at different times and by different observers; much more probably, in its basic nature, this *Proteus* is the same everywhere.

Paleokinetic Phenomena in the Brain

Because of the success of electroencephalography, we have more precise knowledge about paleokinetic processes in the brain. It has been mentioned already that neokinetic spikes reveal themselves in the electroencephalogram as waves of the β-frequency range (tens of hertz). Very gradually, because of a number of complicating factors, these curves transform into a process which is clearly paleokinetic, that is, α-waves with a frequency of about 8 to 15 Hz (perhaps the same group also involves the ultraslow subgroup δ with frequencies of the order of 2 to 4 Hz). The whole picture of relations is much more complex here, as it should have been expected from the brain cortex.

The main difficulties in the interpretation of α-waves center around two factors: their amplitude in the electroencephalogram, and their relation to the states of activity and rest of the hemisphere cortex.

It was noted long ago that β-rhythms are primarily typical of large-cell areas and layers of the cortex (as, for example, the fifth layer of the motor area), while slow waves dominate in small-cell (granular) areas such as the sensory visual area (area striata). Livanov (1934) pointed to the analogy between this phenomenon and what could be expected if brain cells represent plates of condensers in oscillating circuits: Small, numerous, densely packed cells obviously correspond to condensers of higher capacitance, leading to a lower natural frequency of the oscillating circuit. Nevertheless, this is still not more than an analogy.

If cortical cells are considered as independent oscillators, it is first of all necessary to find out which relations among such oscillators can be expected to lead to the phenomena that are actually observed by our oscilloscopes. Let us begin with the small granular fields responsible for the slow oscillations of the α-group.

There are, on average, about a million neural cells in each cubic millimeter of cortical tissue. If all neural cells were oscillators whose frequencies were independent of other cells of the group, that is, if all the frequencies of the α-range (5 to 15 Hz) had equal probability, each cubic millimeter of the cortex would represent all possible frequencies of the range mentioned, with average differences among individual oscillators in the order of one-hundred-thousandth of a hertz. This would lead to a practically flat spectrum with infinitesimally small amplitudes for each separate frequency, that is, something dramatically different from what is observed in actual electroencephalograms.

This means that the numerous oscillators of the small-cell areas influence each other and attract one another into large constellations that demonstrate a single frequency, typical for the whole complex. It is necessary to find out whether such frequency synchronization is possible without concurrent phase synchronization.

Precise mathematical analysis of a multitude of oscillators working at the same frequency but with arbitrary, equally probable phases shows that the ensuing interference decreases the amplitude of the oscillations, down to a disappearingly small residual, and that, according to probability theory, this attenuating effect grows dramatically with an increase in the number of oscillators. So, long before the number of oscillators working together at the same frequency reaches the tens or hundreds of thousands seen in each cubic millimeter of the cortex, this interference will decrease the amplitude of their oscillations to infinitesimal fractions of the sum of the amplitudes of the oscillators.

To simplify the calculations, let us consider a more simple case when each oscillator can have only one of two opposite, equally probable phases (for example, $0°$ and $180°$). In this formulation, the problem is equivalent to the well-known problem of the probability of a certain combination of "heads" and "tails" during a simultaneous toss of a large number of coins. Analysis shows that the sum of the products of the resultant amplitudes of the oscillations with the probability of the oscillations (i.e., what is called the mathematical expectation of the resultant amplitude) equals[28]

$$2n \times U_{2n} \times 2^{-2n}$$

where $2n$ is the number of oscillators, and

$$U_{2n} = \frac{1 \times 2 \times 3 \times ... \times 2_n}{\left(1 \times 2 \times 3 \times ... \times n\right)^2}$$

Table 1 Resultant Amplitudes Disappear Without Phase Synchronization

Number of oscillators	Mathematical expectation of amplitude	Its relation to the total number of oscillators
24	3.8683	0.1611
100	6.7741	0.07677
400	13.5736	0.03393
1,600	27.1603	0.01698
6,400	54.3206	0.00849
25,600	108.6412	0.00425

is the coefficient in the middle term of Newton's binomium in the power $2n$. Let us show a table of values of mathematical expectations and their ratios with respect to the total number of oscillators for different, increasing values of $2n$ (Table 1). The first value gives the magnitude of the most probable, average resultant amplitude, while the second value shows which fraction of the actual amplitude of each oscillator reaches the electrodes of an oscilloscope if phases of oscillations are independent.

The table shows that, for example, if there are 25,600 independent oscillators, the electrodes will actually feel only 108 (about 0.4% of all oscillators) while the remaining 25,492 cancel each other by interference.

Thus, by the method of exclusion,[29] we conclude that there has to be an inevitable synchronization, both by frequency and by phase, of numerous low-frequency oscillators in the cortex. It is necessary to add here that we do not know a single actual physical example of oscillators entraining other oscillators that were in resonance with the first group,[30] except in the presence of a perfect phase relation, and we cannot imagine how this could happen otherwise.

From here, it follows rather simply that, since the number of cortical low-frequency oscillators is three orders of magnitude higher than the number of large-cell high-frequency oscillators responsible for the beta frequency range, and since all the oscillators of a given low frequency are synchronized by both frequency and phase so that their amplitudes are summed up, oscillations of the alpha range are picked up by electrodes as signals a thousand times larger than oscillations of the beta range. Undoubtedly, this is the reason that these inherently microvolt processes reveal themselves in an encephalogram as exceeding the beta-spikes in their amplitude.[B]

In the muscle, both neokinetic millivolt spikes and paleokinetic, tonic, slow microvolt waves are produced by the same number of mions[31]; therefore, it is quite understandable that, in an electromyogram, the latter are overshadowed against the background of the neokinetic tetani, up to their total indiscernibility.

Paleokinetic Function[32]

The second difficulty[33] in interpreting alpha-waves in cortical bioelectric curves is related to the problem of their physiological significance, and there exists a whole

set of interpretations that are more or less similar in their basic assertions (Adrian, 1939; Kornmüller, 1937; Livanov, 1934; Rohracher, 1940; and others). It is sufficient to consider alpha-waves as possessing features typical of paleokinetic processes, and one will obtain all the results of clinical observations and experiments as particular consequences of this main thesis.

Action currents, spikes, and beta-waves can be recorded from any axon, in particular from conduction pathways of the white matter of the brain. However, experiments with needle electrodes, isolated along their whole length except the very tip, show that alpha-waves exist only in the gray cellular matter and immediately disappear after the electrode enters the white matter. This means that beta-processes, as is typical of neokinetic waves, propagate along conduction pathways in the "axon" manner. In contrast, alpha-processes spread over the cortex (or subcortical ganglia) as over a neuropile in a diffuse, irradiation, "dendrite" manner (with velocities not exceeding a few centimeters per second).[34]

It is possible that most of the small cells of granular fields (as well as brain stem small-cell nuclei) do not send their axons into the white matter but represent components of ancient, neuropile structures. The oldest areas of the cortex (archipallidum,[35] palaeocortex) consist of small cells as do the oldest areas of several nuclei of a variety of phylogenetic ages (paleorubrum, related to the vermis parts of the dentate nucleus). On the other hand, cellular groups that serve as the sources of long, effector axons consist of large cells (the fifth layer of the pyramidal field, the pallidum, striatal effector cells, areas of the nucleus ruber which give birth to the Monakow's tract, etc.). These are obviously all forms of neokinetic substrates.

Alpha waves were interpreted as waves of "rest" because they disappear during sensory or effector stimulation of the cortex or during emotional excitation of the subject. Rohracher (1940) convincingly explained the difficulties of recording alpha-waves in animals by the fact that the state of an animal who is tied to an experimental frame and who has just gone through a trepanation without narcosis (which distorts the electroencephalographic picture) is very far from quiet rest.

The problems are that (a) when the brain is actively involved, alpha processes can be eliminated for not more than a few seconds, after which time these processes stubbornly come back, and (b) in states maximally close to undisturbed rest—in sleep—alpha processes disappear. It is hard to disagree with Rohracher, who argued that if alpha waves reflect assimilation and resynthesis, it is as hard to suppress them for a long time as it is to stop breathing; during sleep, however, resynthesis is reduced because at lower levels of basal metabolism and during brain idling, dissimilation is low. Actually, Loomis and Harvey (1938) were able to record alpha-waves in a sleeping person during bright, active dreams.

From our point of view, alpha-waves represent a bioelectrical "glitter" of the very same humoral, paleokinetic control processes that were described earlier for both lower levels of the autonomous nervous system. On the one hand, these are secondary trace processes of resynthesis, regulation of excitability, and tonic sensory corrections; on the other hand, these are processes of preparatory, anticipatory settings that prepare the route for the following neokinetic, effector phase waves.

Primary or Anticipatory and Secondary or Corrective Regulations

In all the subdivisions of the autonomous nervous system, and using the same substrate, we witness two processes. One of them is seen as trace potentials,

electrotone, and alterations in the axon; slow potentials, the "intermittent factor" of Barron and Matthews (1934, 1935), subordination, facilitation, CES and CIS, and Sechenov inhibition in the spinal cord; and alpha-processes in the brain cortex. All these phenomena are indistinguishable from processes in autonomous systems and in the diffuse nervous system of lower invertebrates in three ways:

- Having both signs, being slow, and being characterized by microvolt amplitudes
- Lacking the all-or-nothing law, refractoriness, and phase waves
- Displaying humoral nature, summation, iterative nature, and irradiation

Since the emergence of (a) the telereceptive function of the head end of the body, (b) the integrative function of the nervous system, (c) jointed skeletons and striated muscles, and (d) neokinetic, "telegraph" spike processes, bioelectrical by nature,[36] this ancient, humoral paleoprocess has regulated the powerful but blind[37] discharge of the neo-spike, which is extremely limited in four areas:

- Space (principle of isolated conduction)
- Time (from latency to refractoriness)
- Dynamics (all-or-nothing law)
- Sign (only electronegativity)

At all levels, these regulations proceed according to two types: as secondary corrections and adjustments (a post factum type) and as preliminary settings and anticipations (an ante factum type). Post factum regulations are easier to detect and can be seen in three areas:

1. At the peripheral level, as the electrotonic central control of the characteristics of excitability and conductivity, and also of the parameters of excitation; in the skeletal muscle, as the control of the humoral, paleokinetic component of tone (further, we are going to mention the existence of other types of tone[38]), as a characteristic of muscle excitability as well as of its mechanical parameters such as unloaded length, coefficient of stiffness, and viscosity; in the moton,[39] as a whole, as control of the dynamics of the process of excitation by controlling both force and velocity thresholds and optima, and the all-or-nothing ceiling.
2. In the ventral horn, as all the aforementioned types of specific selective inhibitions.
3. In the cortex, as alpha phenomena. The alpha process apparently controls spike beta-waves electrotonically with respect to both their amplitude (sometimes, one can see with the naked eye a decrease in beta-wave amplitude in an encephalogram when large alpha-waves shift toward positive potentials, and a 1.5- to 2-fold increase in the amplitude of the beta-waves when alpha-waves move toward negative potentials) and their propagation in some directions and blocking in other directions, that is, by the creation of working constellations and dominant foci. It is quite possible that these excitatory–inhibitory alpha constellations, which determine the direction of neokinetic impulses, are closely related to stable foci of cortical excitation and inhibition as described by Pavlov.

Preliminary and anticipatory regulations of the second type (ante factum) probably take place at all the levels of organization of the nervous system and are not limited to having a single physiological tool—the paleokinetic process. Within the context of the present paper, let us focus only[40] on paleoregulations:

1. At the peripheral level, the discussed anticipatory, regulatory settings are actually identical to the adaptive–trophical process[41] that was discovered by Orbeli and his school and was localized in the sympathetic, neural substrate. The same group of regulatory phenomena involves the effects of stimulation of nn. sympathici upon muscle fatigue.
2. Within the spinal cord system, one has not been able to name with certainty a single mechanism from the adaptive–regulatory area.
3. As one could have predicted *a priori*, in the area of cortical activity, ante factum regulations are particularly numerous and divergent. They reveal themselves in electroencephalograms, in the results of analyses of clinical observations, and, sometimes particularly clearly, in correlations of electroencephalograms recorded from different cortical zones simultaneously with electromyograms. For example, it is commonly observed that the initiation of a centrally originating, long-lasting tetanus in a skeletal muscle is accompanied by a precisely timed ("spike in spike") chain of beta-waves in the motor cortex that later completely disappear. Obviously, continuation of the tetanic process in the muscle is supported by lower, extrapyramidal levels, while the pyramidal zone, in this particular instance, plays only the role of a trigger. These cortical triggers, whose dysfunction in hemipareses is so detrimental for voluntary movements, and which, on the contrary, overstrain in clinical pictures typical of Parkinsonism, certainly belong to the same group of regulations.[C]

The same group includes a variety of setting processes that sometimes reveal themselves as brief (apparently subthreshold) tetanic discharges in the electromyogram that do not lead to any discernible mechanical activity of the muscle. The same class of phenomena involves intentions, bioelectrical events in the cortex and in the muscle that accompany the intent to perform a movement, imagining the performance of the movement, and so forth. Concealed synkinesias are very close to intentions. Apparent synkinesias, that is, involuntary accompanying movements of muscles or limbs[D] that are unnecessary for a given task and sometimes impossible to suppress, always belong to the area of motor pathology. However, accompanying innervations of adjacent muscles and contralateral limbs that reveal themselves as muscle biocurrents ("synneiries") without an external motor effect are absolutely normal and, in a sense, helpful for the ongoing movement, although it is still impossible to assess their usefulness.

Finally, it is very probable that the paleokinetic group includes one extremely important central process that plays a major role in phenomena of automation. A number of central neural effector structures (this has been most convincingly established for the premotor fields of Brodmann Area 6) are not effectors in the direct meaning of the word but rather establish connections between the higher cortical levels that play the leading role for a given motor act and the lower, subcortical levels that take the responsibility for background, technical automatisms. As demonstrated by focal pathologies of premotor fields, these areas put the lower

levels into action, stimulate them to develop certain auxiliary skills or automatisms, and provide timely ecphoria of already developed automatisms.[E] All these belong to actions within preparatory, setting, adaptive processes, and there are reasons to classify "alpha" phenomena as belonging to the same class of events.

The Problems of Inhibition, Tone, and Rest

Three urgent problems that are similar in form are facing contemporary neuro-physiology. These problems require, if not solutions, then, at the very least, order and classification of the notions that belong to these problems and a clarification of terminology. All three problems have become sharpened to a limit[42] because of the abundance of accumulated facts and the artificial fitting of the permanently increasing host of phenomena into standardized frames. These are the problems of inhibition, tone, and rest.[43]

One need not emphasize how many absolutely heterotypical phenomena have been accumulated with time under the indifferent term "inhibition." This term is used to address the suppression of an electrotonic type; the suppression of excitation; a decrease in the amplitude of excitation (spikes, muscle contractions, gland secretion, etc.) under the influence of inhibitory agents; a normal excitatory process (e.g., the effect of electrical stimulation of the nn. vagi) that induces an inhibitory effect in the target organ (e.g., in the heart muscle); suppression that results from an overexcitation, like in the deep stages of parabiosis (pessimal conflicts); conduction blocks created by the heterochronism of structures that have not lost their excitability; humoral effects of suppression (e.g., Cannon's "sympathies I"); and many more.

There are an equally large number of absolutely different phenomena united under the term "muscle tone"; therefore, it is not at all surprising that this notion has become virtually impossible to define. This group of phenomena include the fully humoral "prä-tone" studied by Uexküll in lower invertebrates; the complex paleokinetic synthesis of humoral–electrotonic shifts of excitatory and mechani-cal characteristics of the skeletal muscle, which has been mentioned earlier and whose mechanical characteristics look like contractions and relaxations of the stri-ated muscle that are similar to the smooth muscle; and two types of the same paleokinetic tone which are so different from each other that it is hard to see in them phenomena of a common genesis: the elastic tone, which increases in cases of cortical hemiplegias, and the viscous tone, which increases in cases of patholo-gies of the intermediate, extrapyramidal level.

The mentioned paleotones are followed by younger but nevertheless obvi-ously tonic formations: tonic contractions that were demonstrated in muscles of decerebrate cats by Briscoe (followed by demonstrations in cats by Gorshkov and Guseva and in decerebrate kittens by Arshavsky) with the help of indirect electri-cal stimulation of subthreshold amplitude and frequency. Given the frequencies used by these experimenters, tone of this type is reflected in the electroencephalo-gram and electromyogram by the frequency range between 15 and 30 Hz. Finally, the same group should include direct transition forms between tone and tetanus, which some authors term "tetanic tone" and which can be observed, for example, during the neck–body statokinetic reflexes of Magnus.

The situation is not simpler with respect to the third of the aforementioned terms, and perhaps its forthcoming deciphering will have most significant conse-

quences for neurophysiology. If one eliminates the basal rest (if it exists not only as an abstraction), which is the only one that deserves its name, all the innumerable other forms of seeming "rest" are thick with concealed movement. This group involves the fine preparation and setting of a motoneuron and its synapses, adaptive trophics in the neuromuscular plate—resynthesis and preparation of explosive phosphates in the muscle itself and regulation of the dynamic balance between acetylcholine and esterase—and so forth. The same group includes the already mentioned concealed synkinesias and synneiries.

Popova's analyses of the biodynamics of child walking in early ontogenesis showed that there is a basic difference between the mechanisms of control of stable step length during the second year of life and in adults. A toddler is unable to control properly the main forward force impulse in the leg ("epsilon"), in combination with the available moment of leg motion and the external force field, to ensure a required step length. To correct step length when the epsilon impulse is too weak or too strong, the child uses an additional impulse, "dzeta," approximately during the first one-third of an initiated step, which leads, in precise relation to step length, to high variability. (Sometimes an increase in the corrective force wave dzeta exceeds the epsilon itself.) Although adults do not demonstrate this "childish dzeta," the stability of stepping is much higher, exclusively because of the anticipatory control of the main wave epsilon, which is beyond the child's abilities.

Our observations of running, using the cyclogrammetric method, have shown that in distal segments of the leg, which have higher moments of inertia with respect to the proximal joints and show accelerations of higher amplitude, there is a very variable background of functional conductance for effector impulses, and that it takes time to develop the art of sending appropriate impulses into the muscles of these segments at proper times—at the optimal moment of conductivity adjustment. At early stages of practice, there are possibilities for the impulse to arrive but not to be conducted.   ·

By comparing these observations with the fact of blocked synaptic conduction in anterior horns by centrally regulated heterochronism (Lapicque), and also with the fact[44] of muscle selectivity with respect to central effector impulses provided by P. Weiss, we conclude that all these represent reflections of a very homogeneous mechanism of preparatory differential adjustment of conduction. In all the cases described, these preliminary adjustments and adaptations proceed on the background of intense, ongoing activity rather than on the background of general rest of the organism. However, in these cases we deal with ante factum regulations, and, with respect to each muscle, these setting processes occur during its diastolic phase, which can represent a state of rest prior to movement initiation or a pause between two episodes of rhythmic activity.

Now, we can only guess at the following:

- The results of studies of rest, as briefly described, in the immediate future. This rest is as different from actual inaction as an undeveloped photographic plate with a concealed image is different from an unexposed photographic plate.
- What exactly plays the role of the "developing solution" for this photographic plate in different cases; what activates and puts into action the invisible contours of an intended movement drawn on the plate.

- The essence of anticipatory adjustments, the adjustments that sometimes start to prepare the nervous system and peripheral effectors to an intended movement way in advance.
- The role of electroencephalography and oscillography in finding answers to these questions.[45]

Bernstein's Notes

[A] During the last few months, the author of this paper had an opportunity to witness a number of absolutely stunning cases.[46] Let me review only two examples kindly demonstrated by L.B. Perelman (Clinics of the Institute of Neurology of the Academy of Medical Sciences).

Patient T., as a result of an extensive injury in the area of the left rolandic fissure, with complications, demonstrated pronounced ataxia of the right arm with intentional tremor against a background of complete anesthesia. He was unable to perform any pointing or grasping movement because of an overwhelming, uncontrolled intentional tremor in his hand. If a rubber band was placed on the affected arm of this patient (remember that he had complete anesthesia), or even a tight ring was placed on his finger, both ataxia and tremor disappeared immediately and the patient could do the "finger-to-nose" test perfectly. If the patient was blindfolded and the physician said, "I have put a ring on your finger," while actually no ring was placed, the tremor persisted as usual. On the other hand, if the patient was distracted by a conversation and a ring was sneaked onto his finger, movements immediately became well organized.

Patient C. had an injury of the left temporal area with residual spastic paresis of the right hand and a pronounced grasping reflex. When any object touched his palm, he grasped it immediately, involuntarily, and could not release it; the more the he tried to release his fingers, the tighter his grip became. It was impossible for this patient to drop an object from his right hand. He was blindfolded and the physician slowly moved a tea saucer, a glass ashtray, or another such object to his affected palm. When the object was 15 to 20 cm from the palm, his arm moved involuntarily and with increasing speed toward the object and grasped it. When wooden objects were used, this effect did not occur, while any objects of the type mentioned were effective in 100% of cases, in different modifications of the experiment. The working hypothesis was that there is a slight feeling of coolness from approaching glass or china objects. Unfortunately, the phenomenon was temporary and was not studied precisely.

Which vivisectionist will even think of such combinations and which experimenter will be able to reproduce them artificially?

[B]If the size of a recording electrode decreases, the ratio of the numbers of small and large cells, whose potentials are recorded by the electrode, will not change significantly.

[C] It is clear that the trigger mechanism consists of (a) a tetanic (beta) part that directly excites the muscle at the very beginning, and (b) an additional part that provokes the continuing support of the initiated tetanus by the extrapyramidal system.

[D]These should be distinguished from synergies, that is, from collective movements and efforts that are normal, purposeful, and necessary for the motor act.

[E]Such organs of the central nervous system could be addressed as automatizers.

Bernstein's References

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Editor's Notes

[1]The paper was translated by Mark L. Latash and edited for clarity. Bernstein presented this material at the Joint Conference of the Societies of Physiology and of Neuropathology, January 20-22, 1945, dedicated to the 300th anniversary of the concept of "reflex." The paper was submitted May 21, 1945, and subsequently appeared in the *Physiological Journal of the USSR,* 31-5/6, pp. 298-311, 1945.

[2]This English summary was part of the original Russian publication. It has been edited for clarity.

[3]In the paper, Bernstein distinguished between *ante factum* and *post factum* regulations (see "Primary or Anticipatory and Secondary or Corrective Regulations"). To avoid confusion between the two, it may be better to read "anticipatory" for "adaptive."

[4]What exactly preceded this "now" is a little unclear in Bernstein's biography. As so many, Bernstein had fled Moscow, in 1941, upon the approach of Hitler's troops (Feigenberg & Latash, 1996). During his self-imposed exile, first in Siberia and later in Kazakhstan, he had no opportunity to do any normal work. The battle of Moscow was relatively short, from November 1941 through January 1942, Russian troops saving the city and pushing back the Germans by about 200 km. Nevertheless, the Muscovites were slow to return, and to our knowledge, Bernstein did not return before the end of 1944. In other words, he was just back before presenting his paper to the Joint Conference in January 1945. Certainly, the text was edited before being submitted (in May), but still, this was his first paper to present a general theory of brain function and it must have taken considerable time to prepare. The measure of his knowledge in the 1945 paper suggests that he had worked on his understanding of the brain during his self-imposed exile. One must assume that his hurried packing before fleeing from Moscow included a bunch of texts on the brain.

[5]There is no doubt that Moscow was in a festive mood after the defeat of Hitler's armies (cf. Aksyonov, 1993-1994). Exactly which anniversary one thought to celebrate, however, remains a bit of a mystery. The idea of involuntary movements was first published by Descartes in 1641 in the *Fourth Set of Answers to Objections* of his *Meditations* (cf. 1953, p. 448). Descartes' "reflected animal spirits" (cf. 1953, pp. 823-824), however, were still a far cry (cf. Canguilhem, 1955) from the "idea of reflex" that Bernstein and his peers regarded as "classical," that is, the stereotyped sequence of receptor, conductor, and effector, which dates from the second half of the 19th century.

[6]To Bernstein himself, there must have been very little to celebrate, since he strongly objected (cf. Bernstein, 1988/1935) to the classical notion of a reflex arc (as opposed to a reflex ring), as well as the Pavlovian idea that single cortical cells are responsible for triggering reflexes. Apparently, Bernstein just took the occasion of the Joint Conference to present a new overall theory of the brain, remaining expediently silent on the idea of "reflex" in the rest of his paper.

[7]In 1863 (cf. 1965), Sechenov had claimed that behavior consists of the unleashing of reflexes that are usually inhibited by the brain.

[8]It is important to realize that Bernstein was strongly influenced by Pavlov, notwithstanding his 1935 objections to deterministic schemes and his 1950 clash with the neo-Pavlovians. The present paper contains the typically Pavlovian emphasis on evolution, and even Bernstein's dichotomy of central nervous function into what he calls "paleokinetic" and "neokinetic" processes is somewhat reminiscent of Pavlov's studies of the adaptive and trophic role of lower levels of the nervous system (cf. Grigorian, 1974).

[9]Note that Bernstein's use of the term *development* includes both ontogenesis and phylogenesis, as did the German term *Entwicklung*.

[10]Section titles have been added for clarity.

[11]This idea goes back in principle to the work of J.H. Jackson (cf. Clarke, 1973), to whom Bernstein does not refer. Similar hierarchical schemes were, however, rather commonplace in Soviet neuroscience. Around 1940 (cf. 1988/1940), Bernstein was strongly influenced by Weiss's static theory of hierarchical organicism (cf. Weiss, 1959/1925) which in this 1945 paper Bernstein starts to transcend by creating a more flexible hierarchy (cf. Bongaardt, 1996).

[12]Note that Bernstein's views, while in principle emphasizing discontinuous evolution, still allow for an arrow of time, some processes being "continuous" or, as he later stated, "slowly progressing."

[13]In early evolution of the nervous system, nonneuronal processes had the lead, neuronal constructions at best forming a "satellite." In the next section, Bernstein depicted a later phase of evolution where neuronal construction took the lead and "the chemical component turned into a satellite."

[14]*Neuropile* can be defined as "a dense feltwork of interwoven cytoplasmic processes of nerve cells (dendrites and neurites) and of glia cells in the central nervous system and in some parts of the peripheral nervous system" (*Dorland's Illustrated Medical Dictionary*, 1965). To Bernstein, however, it was important to define the term less precisely, as the kind of general "background tissue" out of which the neuronal system of "telegraph wires" emerged.

[15]In Weiss's hierarchical view (cf. Note 11), the highest level is fixed for any particular species, for instance, the *cortex cerebri* in humans. By choosing terms such as "leading element," "leading level," or even "leading link" (see Bernstein's summary in the present paper), Bernstein opened the way for more flexibility. In *On Dexterity and Its Development*, written in 1947 (cf. Bernstein, 1996/1991), he not only depicted the evolution of leading levels, such as the *corpus striatum* in birds, responsible for emotions and planning, but also opened the way for the individual organism to choose a particular leading level, depending on the motor problem at hand. After meeting with Gel'fand, Bernstein changed his terminology, replacing "leading element" with "essential variable" and turning the physiology of initiative into a mathematical search theory as to how the animal finds the appropriate essential variable (cf. Meijer & Bongaardt, 1998).

[16] Bernstein's emphasis on coordination (cf. 1988/1935) did not preclude him from viewing the brain as the dominant organ, contrary to what some may have expected in the early days of "self-organization" (cf., e.g., Roth & Meijer, 1988).

[17]Also in the Russian original, this part of the text appears to be woolly and repetitive. We are left with a rather disappointing scheme: The "leading role" was played, subsequently, by (1) the effector function, (2) the telereceptors, (3) the rostal ganglia in the head, and (4) the encephalization of functions. In the 1945 paper, the difference between 2, 3, and 4 is less than clear. With hindsight, one sees Bernstein creating relatively empty

slots, to be filled in later in a much more specific way (see, particularly, Bernstein 1996/1991).

[18]Bernstein's use of the term *substrates* reveals the primacy he gave to function: It is the same function that used a different anatomical substrate. In the next section, he used the phrase "transplanted onto new soil."

[19]Bernstein introduced his "paleokinetic/neokinetic" distinction by side-stepping into clinical neurology and technical advances in neurophysiology. These excursions strike one as having been added at the last moment, revealing Bernstein's genuine enthusiasm for possibilities to "look into" the brain. His father had been a famous psychiatrist, and after the Revolution, Nikolai Bernstein had settled in Moscow as a neuropsychologist. Thus, from the beginning of his career onward he may well have wanted to study movement in order to understand the brain.

[20]This, of course, is where Bernstein himself comes in. In 1945, he was already famous for his studies of movement. This allowed him, a few paragraphs below, to dichotomize the brain not just into "paleo" (old) and "neo" (new) but into paleo*kinetic* and neo*kinetic,* suggesting that understanding movement is of prime importance to understanding the brain.

[21]This notion literally means "working the points" in a railroad track. At the time, Louis Edouard Lapicque (1866–1952) was one of the foremost experts on electrical phenomena in the nervous system. The importance of the kind of changes Bernstein referred to here, that is, slow changes of potential, had also been highlighted in the work of Erlanger and Gasser, who received the 1944 Nobel Prize in Physiology or Medicine (cf. Granit, 1944).

[22]Note that Bernstein had just stated that microvolts were added to physiology during the last "60 to 80 years." He now needed some arguments to show that their evolution was earlier than that of the action potential before he could present his definitive label, "paleokinetic." This distinction between neokinetic and paleokinetic phenomena was unaltered for the rest of his life and featured importantly in his last paper (cf. Meijer & Bongaardt, 1998).

[23]Bernstein's views on muscle tone were very close to the "preparedness" literature of the 1960s (cf. Meijer & Bongaardt, 1998; Pribram, 1971).

[24]The paper was written while molecular biology was in its infancy and the chemistry of life was still largely seen as the chemistry of colloid solutions.

[25]What Bernstein announced here, to be filled in later in the paper, may well be one of its most original messages, that is, the fascinating richness of the roles that are played by the lower levels. In traditional mechanism, the only levels that are worthy of our fascination are the highest ones. Sherrington's "enchanted loom" (cf. 1906), for instance, emphasized the magic of the higher levels of the brain, more or less implying that the lower levels are simple and can be understood with simple, mechanistic schemes. A similar view pervaded the work of Sir John Eccles (cf., e.g., 1978).

[26]Apparently, the action potentials of the "telegraph wires" belong to biophysics, whereas slow microvolt changes belong to biochemistry. Thus, Bernstein missed the physical literature on synchronization of oscillators, which he analyzed in the framework of paleokinetic phenomena (cf. the following subsection).

[27]There have been bitter and polemical discussions concerning some of Bernstein's central ideas and Bernstein's intellectual priority over Sechenov (cf. Mecacci, 1979, p. 92).

[28]To see how this works, take $2n = 4$, and write "0" for 0° phase difference, "1" for 180°. The set of possible states, with the sum of their amplitudes (expressed in units of amplitude) then equals $0000 = 4, 0001 = 2, 0010 = 2, 0100 = 2, 1000 = 2, 001 1 = 0, 0101 = 0, 0110 = 0, 1001 = 0, 1010 = 0, 1 100 = 0, 0111 = 2, 1011 = 2, 1101 = 2, 1110 = 2,$ and 1111

= 4. The sum of these amplitudes ($2n \times U_{2n}$) = 24, while there are 16 possibilities (2^{2n}), so the resultant product equals 24/16.

[29]In Bernstein's famous 1935 paper (1988/1935), he used indirect proof in deriving the mathematics of coordination.

[30]Bernstein may have missed the letter Christiaan Huygens wrote to his father on February 26, 1665, where Christiaan described how two clocks, hanging on the wall in close proximity to each other, tick in synchrony, apparently due to an "imperceptible agitation of the air" (Société Hollandaise des Sciences, 1893, pp. 243-244). More seriously, he missed Van der Pol's nonlinear theory of electric oscillations, which largely dealt with synchronization (e.g., 1934). Most astonishing, however, is that Bernstein failed to mention Andronov and Chaikin's *Theory of Oscillations,* which was published in 1937 (cf. 1949/1937). See also Note 26.

[31]Bernstein used the term "moton" for motor unit, that is, a particular motoneuron and its bunch of muscle fibers (the "mion").

[32]In his own summary (see the beginning of the paper), Bernstein gave as his third argument "the mainly executive role of neo-kinetism and the adaptive regulatory role of paleokinetism." In the text itself, however, the executive role of neokinetic spikes was hardly discussed. Maybe it was taken for granted, Bernstein's main argument then being concerned with the function of paleokinetic phenomena.

[33]This difficulty in the interpretation of alpha waves was characterized above as their "relation to the states of activity and rest of the hemisphere cortex."

[34]This comes very close to the central thesis of Pribram (1971).

[35]Bernstein probably meant "archipallium."

[36]Note how Bernstein linked these four factors: Because we have receptors in our head, whole-body movements could be integrated from the brain, while at the same time they were made possible by the evolution of the vertebrate locomotor apparatus, necessitating the quick transport of signals through "telegraph wires." In *On Dexterity and Its Development* (cf. 1996/1991), he depicted how reptiles, the first to be able to inhibit movements, had the problem of cold-bloodedness and thus slow transport of signals. Motor control, therefore, had to be a function of the spinal cord, the brain just being too far away. According to Bernstein, this was one cause of the destruction of dinosaurs (pp. 84-88).

[37]This may well be the most amazing single statement in this 1945 paper. Just after we learned that alpha waves are "bioelectrical glitter," the executive neokinetic spikes turn out to be "blind." *Dorland's Illustrated Medical Dictionary* (1965) defines *neokinetic* as "a term applied to the nervous motor mechanism regulating voluntary muscular control." True, Charles Darwin had identified free will with chance—"I verily believe free will & chance are synonymous.—Shake ten thousand grains of sand together & one will be uppermost,—so in thoughts, one will rise according to law" (Gruber, 1974, p. 243), a thought which strongly influenced 20th century psychology (Boakes, 1984). Nevertheless, neurophysiology was largely deterministic, and Bernstein's "blind executive" may well turn out to be the strongest statement of the stochastic nature of the brain before Edelman's *Neural Darwinism* (1987).

[38]Cf. the next section.

[39]Cf. Note 31.

[40]Apparently, this "only" should not be taken literally: In what follows, Bernstein also provided examples of neokinetic anticipation.

[41] Bernstein, in agreement with the embryological literature on the development of motoneurons, regarded the "adaptive–trophical process" as anticipatory, that is to say, not dependent upon sensory information. For the kind of mechanism involved, see Edelman (1988).

[42]According to the translator (MLL), Bernstein's language is very emotional here.

[43]Although at first sight these topics appear to be unrelated, Bernstein's earlier statements about the nature of "rest" reveal why he took these three topics together. Contrary to what many appear to suggest, the central nervous system is a beehive of activity—as shown by electroencephalography. Neurons "at rest" are in fact active, maintaining a negative membrane potential. Muscles "at rest" have tone and are thereby ready, so to speak, to be activated. Complete (re)actions are waiting to be released from inhibition.

[44]This "fact" reveals that Bernstein was still very much under Weiss's spell. According to Weiss, motoneurons have specific antennae for control signals, the left biceps, for instance, just picking up the signals that are meant for the left biceps (cf. Weiss, 1936 & 1980/1941). Whether right or wrong, this view was never widely accepted, and it certainly was no fact.

[45]If one accepts this 1945 paper as Bernstein's first publication on the central nervous system, it may be appropriate here to shortly digress into what was to come. In the second half of the 1940s, much of Bernstein's activity involved study of the brain. Of his translated works, *On Dexterity and Its Development,* written in 1947 (cf. 1996/1991) clearly shows how much his views on the evolution of the brain had matured. Bernstein there emphasized the ability of animals with a cortex to solve new motor problems. To him, it was a more or less logical step to subsequently analyze how animals take the initiative, which is what occupied him through the 1950s and 60s. First, he concluded that animals create a stochastic "model of the future" to then go for one option for the full 100%. After having met Gel'fand (cf. Gel'fand & Tsetlin, 1961), Bernstein changed his phraseology into animals realizing the correct value of an essential variable. His last paper, written in 1966, has a title which is very close to that of the present paper: "The Immediate Tasks of Neurophysiology in the Light of the Modern Theory of Biological Activity" (Meijer & Bongaardt, 1998). In it, we find a clearer integration with his views on coordination than in the present paper and a more explicit rejection of the neo-Pavlovian concept of reflex. Again, the paper was inspired by evolution, and the distinction paleokinetic/neokinetic was still part of his theory, in a way with more conviction then, because by then it had been accepted in the West. Of course, the biology of activity was new in the 1996 paper, and he presented a new urgent problem, that is, the theory of biological displays. But that is Bernstein: Consistently working on movement and its importance to understand the brain while all the time throwing out new questions to the scientific community. In a personal conversation, Anatol Fel'dman stated that Bernstein will be remembered because of his questions.

[46]One must surmise that Bernstein saw these clinical cases after his return to Moscow and before he submitted the paper. As an Oliver Sacks *avant la lettre,* Bernstein collected stunning cases long before he could give them a place in any theoretical framework.

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