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Ivane Beritashvili: Founder of Physiology and Neuroscience in Georgia

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This paper is dedicated to one of the outstanding scientists of the twentieth century—Ivane Beritashvili. He was a Georgian physiologist who graduated from St. Petersburg University and worked under the supervision of N. Wedensky. He founded the Department of Physiology and the Institute of Physiology at the University of Tbilisi, Georgia. Among his numerous contributions was the discovery of the rhythmical course of reciprocal inhibition in spinal reflexes, the first demonstration of the excitatory and inhibitory reactions in the brain stem neuropil. But Beritashvili's most significant contribution was the discovery of the mediation of animal psychoneural behavior by image-driven memory.

Keywords animal behavior science, conditioned reflexes, higher brain functions, image-driven memory, neurophysiology, psychoneural behavior, spatial orientation, spinal reflexes

Introduction

Fundamental studies of the nervous system have been ongoing since the nineteenth century. However, a new era in nervous system and brain research began in the middle of the twentieth century when various biomedical disciplines investigating the nervous system worked synergistically, sharing a common language, common concepts, and a common goal — to understand the structure and function of the normal and abnormal brain. One of the most creative of the scientists who contributed greatly to this progress was Ivane S. Beritashvili, the founder of the national school of physiology and neuroscience in Georgia.[1] In 1958–1960 together with Herbert Jasper, Henri Gastaut, Alfred Fessard, and others he was one of the founders of the International Brain Research Organization (IBRO).

For more than a half-century of his activity, Beritashvili was considered a leader among neurophysiologists of Central and Eastern European countries and the former Soviet Union. In the study of higher brain functions he tried to bridge the gap between physiology and psychology and did much to bring them closer together. Following his initial research on the physiology of central coordination (Beritov, 1916), Beritashvili started his investigation of conditioned reflexes. His research was motivated by a disagreement

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[1]Beritashvili is a Georgian family name. The Russian version of the name is spelled variously as Beritov or Beritoff, depending upon the Russian or the German and English publications and sources respectively.

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with I. P. Pavlov concerning the physiological bases for the formation of conditioned reflexes. In the late 1920s Beritashvili came to the conclusion that the Pavlov-Bechterev conditioning situation, with the great restrictions it placed on the animal's behavioral repertoire, was not a proper model for the study of the Pavlovian concept of so-called "higher nervous activity." Instead, Beritashvili came to prefer the method of "free movement" of the experimental animal. His theory of animal psychoneural activity, first summarized in Beritov (1932), and then extended in his next books (Beritov, 1947; Beritashvili, 1965, 1971), bears a strong resemblance to the concept of the "cognitive map" initially developed by E. C. Tolman (1932). Although severely criticized in the early 1950s for his unorthodox theories (*vis-à-vis* Pavlov), Beritashvili contributed greatly to the science of animal behavior by his doctrines on psychoneural activity and image-driven memory.

The vast international turmoil and antagonism that prevailed throughout most of his scientific life, plus barriers of language, which he strove so hard to mitigate, ultimately conspired to limit the influence of Beritashvili's extraordinarily important and unique ideas and relegate them to relative obscurity. Fully appreciated, they should have had a major impact on the study of animal behavior and memory. Their attractiveness is certainly enhanced by knowledge of the fact that their author evolved them a lifetime of rigorously controlled and highly imaginative experimentation (Doty, 1975).

Concise Biography

Ivane S. Beritashvili, the son of a priest, was born on December 31, 1884, in the small village Vegini in Kakheti, in the Eastern region of Georgia (at that time part of the Russian Empire). He studied for the priesthood first at the ecclesiastic school in Telavi, the main city of Kakheti, and then at theological seminary in Tiflis (Tbilisi) the capital of Georgia. Because he came to dislike the prospect of becoming a priest, the young Ivane took examinations for the school-leaving certificate at the 2nd Tiflis gymnasium in 1906. In the same year he matriculated into the Natural Division of the Department of Physical and Mathematical Sciences of St. Petersburg University.

It is very interesting to note here that the outstanding Russian physiologist Ivan P. Pavlov (1849–1936) was also the son of priest and also studied for the priesthood before matriculating in 1870 into the same Natural Division of the Department of Physical and Mathematical Sciences of St. Petersburg University. Both Ivans investigated conditioned reflexes and the Georgian physiologist always competed with Pavlov and Pavlov's school in the study of higher brain functions and animal behavior (Tsagareli, 2003, 2004).

Beritashvili began his experimental research early, as a third year student under the supervision of the eminent Russian physiologist Prof. N. E. Wedensky (1852–1922), who was also the son of priest who had studied for the priesthood. The international neurophysiological community knows Wedensky for his discovery of the phenomena known in Russian as "optimum" and "pessimum." In 1903, Wedensky proposed using the latter inhibitory phenomenon to explain the observation that increasing the frequency of peripheral nerve stimulation initially extended the excitatory response of nerve-muscle preparation but eventually resulted a single contraction followed by complete relaxation ("Wedensky inhibition"). Beritashvili studied the problem of reciprocal innervation of skeletal musculature in frogs showing that local strychninization of the dorsal horn did not disrupt the coordination of the "wiping" reflex. The results of his first work were published in 1911. In the preceding year he graduated from the university and was invited by Wedensky for the first 2.5 years and then for a further 2 years to work in the University Physiological Laboratory.

Figure 1. Ivane Beritoff – as a student of St. Petersburg University (1910).

At the recommendation of Wedensky, Beritashvili left for Kazan in autumn 1911 to work with Prof. A. P. Samoilov (1867–1930) to master the method of registering electric currents in nerves and muscles by the string galvanometer that, in turn, Samoilov had learned from Willem Einthoven (1860–1927) in Leiden in 1904. Later, in the spring of 1914, again with Wedensky's support, Beritashvili joined Rudolf Magnus (1873–1927) in Utrecht to study the techniques of mammalian neurosurgery (decebreration, sectioning the dorsal roots, etc.), the principles of body posture and tonic neck and labyrinthine reflexes in mammals (later the Magnus–de Kleijn reflexes). At the start of the World War I Beritashvili had to cease his research and return to St. Petersburg.

It should be emphasized here that, as Mary A. Brazier remembered in August 1962, during the International Congress of Physiological Sciences in Leiden, when accompanied by Otto Magnus and William Storm van Leeuwen, Professor Beritashvili with his wife visited the grave of Rudolf Magnus, "As we stood among the trees, listening to the eulogy, read by Beritashvili in German, the memories of a happy scientific collaboration came across the intervening half-century with poignant nostalgia." And, "Magnus's comprehensive book entitled *Körperstellung* had not been translated into English, but on that August afternoon in the Dutch graveyard Professor Beritashvili presented to Magnus's son a complete translation of this famous book into Russian" (Brazier, 1975, pp. 24, 26).

In 1915 Beritashvili had to leave St. Petersburg and move to Odessa as a Senior Assistant to Prof. V. V. Zavyalov at the Chair of Physiology in the Physical and Mathematical Department of Novorossyisk University. This Chair was established by Ivan M. Sechenov (1829–1905), regarded as the founder of Russian physiology, who had held the Chair for six years, from 1870 to 1876. One year later, after Beritashvili had been appointed a private docent, he began giving lectures in the course on the physiology of the

nerve-muscle system. During that period he studied defensive reflexes in dogs by the method of V. M. Bechterev (1857–1928).

After the Russian Revolution in 1917, Georgia attained freedom and independence for the short period between 1918 and 1921. During it, in 1918, Ivane Javakhishvili established the first University of Tiflis and Beritashvili received an invitation to organize its physiological department and the course instruction in physiology. In 1919 he set up this Department and from that time onward Beritashvili succeeded in progressively developing intensive physiological teaching and research in Georgia. By 1920–1921 he had published in Tiflis the first Georgian-language textbook on physiology, in two volumes and with a practical guide, and in 1922 in the Russian language. At the same time, he founded a physiological research laboratory and started intensive work. Beritashvili thus realized what for Ivane R. Tarkhnishvili (Tarchanoff) (1846–1908), the Georgian-Russian physiologist discoverer of the psychogalvanic reflex, had been only a dream—to establish a laboratory in his native land. Tarkhnishvili had died in St. Petersburg the same year that Beritashvili came there as a student.

Later, in 1937, Beritashvili published a comprehensive handbook in Moscow in Russian entitled *General Physiology of Nerve and Muscle Systems*. For this book he was awarded the Stalin Prize in 1941. Later revised and enlarged—in 1947 and 1959—this book guided many generations of "Soviet" physiologists. A number of other fundamental handbooks, *General Physiology of the Central Nervous System*, the second edition in 1948 and the third revised and enlarged edition of 1966, and *Structure and Function of the Cerebral Cortex* of 1969, were also published in Moscow in Russian.

In 1935, at the Tbilisi State University, Beritashvili established the laboratory of physiology in the research Institute of Physiology, which now bears his name and honors his dedication to neuroscience. Later, in early 1941, the institute affiliated with the Georgian Academy of Sciences. Very soon the institute became a leading center for physiology and nervous system research in the Soviet Union and eastern European countries. At the same time Beritashvili organized the publication of the Transactions (Proceedings) of the Institute of Physiology, the first volume of which appeared in 1936.

During this period Beritashvili was one of the organizers and founders of the Georgian Academy of Sciences. He was initially Head of the Biological Division of the Caucasian Branch of Academy of Sciences of the USSR (1933–1941), and after the foundation of the Georgian Academy of Sciences he was Head of its Department of Biomedical Sciences (1941–1974).

In 1938 Beritashvili was awarded the Pavlov Prize for important contributions to the study of the peripheral and central nervous systems, higher brain function, and animal behavior. In 1962 he was also awarded the Sechenov Prize for his book *Neural Mechanisms of Higher Vertebrate Behavior*, which, with the support of H. Jasper, was translated from Russian into English and published in Boston (Beritashvili, 1965).

In 1939 Beritashvili established the Georgian Society for Physiology, Biochemistry and Pharmacology (since 1957 the Georgian Physiological Society). In the same year he was elected an Academician of the Academy of Sciences of the USSR and in 1944 became a founding member and an Academician of the Academy of Medical Sciences of the USSR. Beritashvili was an honorary member of many national and international professional societies, among them the American Society for Electroencephalography (1947), the International EEG and Clinical Neurophysiology Federation (1954), the New York Academy of Science (1959), the International Brain Research Organization (IBRO, 1960), the Collegium Internationale Activitatis Nervosa Superioris (1968), and the Society for Biological Psychiatry (1969).

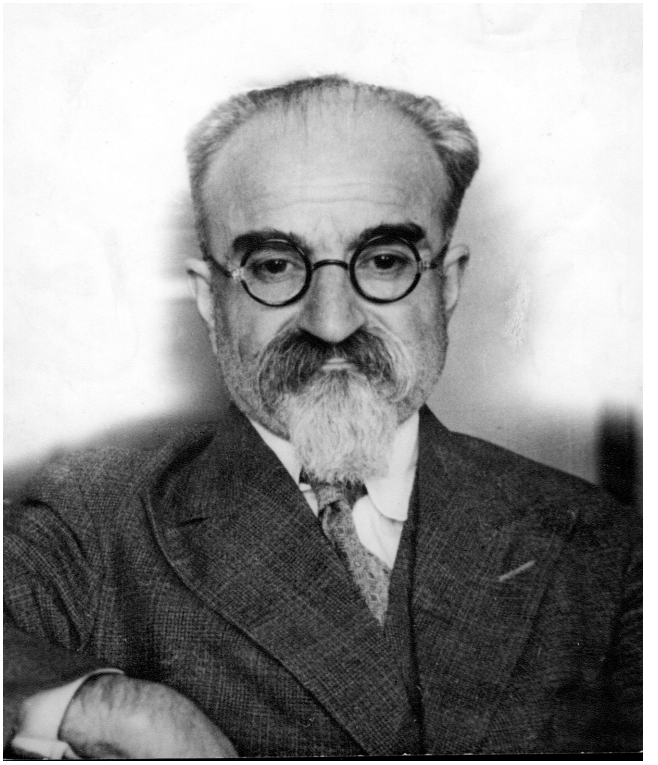

Figure 2. Ivane Beritashvili – the founder of Institute of Physiology (1935).

During his long life Beritashvili was the author of almost 400 research and review papers, many chapters in books, a dozen monographs, and the comprehensive three-volume handbook and the two-volume textbook that were republished many times. He wrote his first book in 1916, at the age of 32, and his last, revised and expanded, was published in 1974, the year of his death when he was almost 90 years old. Shortly after his death, the first selfedited comprehensive book of Beritashvili's selected works was published in Moscow (Beritashvili, 1975), and the second enlarged selection, devoted to his centennial, was released in Tbilisi (Beritashvili, 1984).

Like Ivan Pavlov, Ivane Beritashvili died of acute pneumonia on December 29, 1974, two weeks before his 90-year jubilee. He was buried in the square of Tbilisi State University, alongside the founder of the university, Ivane Javakhishvili.

Beritashvili in St. Petersburg

Ivane Beritashvili's scientific genealogy originates in the physiological school of St. Petersburg University where, in the physiological laboratory then headed by Nikolai E. Wedensky, he grew to become an excellent neuro-physiologist of international stature. He then successfully used the knowledge he gained there to found the Georgian School of Physiological and Neuroscience in Tbilisi (Grigoryan, 1986).

As a student, Ivane Beritoff joined Wedensky's laboratory in April 1909, after finishing his practical studies in physiology. During that time Wedensky examined the influence of various drugs on the centers of spinal reflexes in frogs and gave Beritashvili the task of

investigating the influence of the local application of strychnine on reflexes. It is interesting to note that student Beritoff passed the examinations in all subjects for the third and fourth years, so that in the last year of his education he did not attend lectures and worked only in the laboratory, and very hard. After one-and-a half-years of research he presented the results of his graduation work, which were later published in the form of research articles. As Beritashvili recollected in 1969, he was awarded the first-class diploma for this graduation work (Beritashvili, 1991). These facts clearly emphasize how enthusiastic and zealous was the young Ivane.

Indeed in these first publications Beritoff appeared as a courageous and independent scientist while still being a student. It is very important to underline here, that to study the reciprocal innervation of skeletal musculature he went beyond Sechenov's work on general inhibition.

The year when Beritoff matriculated at St. Petersburg University (1906), the first volume of the Proceedings of the Physiological Laboratory of St. Petersburg University edited by Wedensky was released. Wedensky's paper "Excitation and inhibition of the reflex apparatus in strychnine poisoning" published in this volume initiated a new approach or era in laboratory research: the investigation of the interaction between the processes of excitation and inhibition in the cerebrospinal coordinative centers in strychninization. Wedensky and his school explained these processes by his theory of "parabiosis," that sensory nerve excitability was defined only by the power and frequency of the stimulating electric current. Beritoff's conclusion was discrepant with Wedensky's concept (Grigoryan, 1986). In his first paper "Reciprocal innervation of skeletal musculature in local strychnine poisoning" (1911), Beritoff showed that poisoning only one segment of the spinal cord strongly increased its reflex action, and the nature of the interaction of the processes of excitation and inhibition was defined solely by the activity of the spinal cord coordinative "apparatus." He supposed that, apart from the effect of power and frequency, stimulation of the receptive field of flexion in strychnine poisoning merely strengthens the flexure reflex (Beritov, 1916).

Furthermore, contrary to the expectations of Wedensky and many others, Beritoff demonstrated that reciprocal inhibition does not arise from a weak form of excitation but must instead be, as Sherrington proposed, the exact opposite of excitation. When stimulation of two sensory nerves, one of which evoked excitation while the other induced inhibition of the given muscle, were combined, single action potentials or their groups were either regularly eliminated from or weakened in the electromyogram of the excited muscle in the rhythm of the inhibitory stimulation. Beritoff was so enthusiastic about these results that he wished to inform Sherrington of them by cablegram, but he was dissuaded by his instructor, Prof. A. A. Ukhtomsky (1875–1942) (Beritashvili, 1966; Doty, 1975). The similarity of the wiping reflex to the stretch reflex in the cat obviously appealed to Beritoff, for he was much influenced by the work of Sherrington (Doty, 1975).

The first volume of the *Proceedings* of the Physiological Laboratory of St. Petersburg University was released in 1906, the same year Charles Sherrington's famous book *The Integrative Action of the Nervous System*. Hence the problem of the innervation of skeletal musculature was simultaneously elaborated in two laboratories, by Wedensky in Russia and by Sherrington in England. Beritoff learned English to read Sherrington's book, which had a great influence on the further work of Wedensky's laboratory and on Beritoff himself. It is noteworthy, that the young Beritoff received two very positive references from Sherrington regarding the papers he published in *Pflüger's Archive* (Grigoryan, 1986).

E. D. Adrian, who shared the 1932 Nobel Prize with Sherrington, later recollected in his letter that appeared in the collection of papers dedicated to Beritashvili's 90th birthday, "But my own acquaintance with the work of Professor Beritoff goes back to an earlier period — to the year of 1913, when he was aged 28 and I was aged 24. Beritoff worked, I believe, in the laboratory of Professor Wedensky in St. Petersburg (Leningrad) and I was a pupil of Keith Lucas in Professor Langley's department in Cambridge. Beritoff and I were both concerned with impulse conduction in nerve fibres. To record the 'current of action' in nerve or muscle Keith Lucas used a 'capillary electrometer' much of which he had constructed himself, but we were both impressed by a paper by I. S. Beritoff, entitled 'Zur Kenntnis der Erregungsrhythmik des Nerven- und Muskelsystems', *Zeitschrift fur Biologie, 62* Band, 1913. Beritoff had used the Einthoven String Galvanometer, which was sensitive enough to show the form of the action potentials in a nerve trunk, provided that all the nerve fibres were in action together" (Adrian, 1975, p. 22).

As has been mentioned, in that first paper Beritoff came out against his professor's theory of parabiosis and described the processes of excitation and inhibition as independent phenomena — *sui generis*. This conclusion was expressed more strongly and definitely in his first monograph *Theory on Basic Elements of Central Coordination of Skeletal Musculature* (Beritov, 1916) presented to the Council of St. Petersburg (Petrograd) University as the dissertation for his master's degree. Looking at this comprehensive book one is convinced of its suitability for the doctoral degree.

In April 1917 Pavlov gave a very positive and flattering reference to Beritoff's book, particularly emphasizing his discovery of the rhythmical character of reciprocal inhibition, and highlighting that "Generally, in the works of this young physiologist his critical thinking, powerful initiatives, experimental skillfulness and creative enthusiasm could hardly be overlooked" (Cited by Grigoryan, 1986, p.14). Beforehand, however, the St. Petersburg University Council had not permitted Beritov to defend his thesis because Wedensky was critical of it. On the one hand it is noteworthy how the publication of the monograph, containing sharp commentaries on Wedensky's basic doctrine of parabiosis, and undisguised criticism of the scientific creed of his mentor, testifies to the independence of the research and scientific thinking in the St. Petersburg physiological laboratory. On the other hand, in all probability Beritoff had to leave the university at the end of 1915, and St. Petersburg as well, because of the monograph. In a letter to Samoilov he described the hard conditions under which he lived and had written it. At the same time Beritoff expressed his innermost scientific ideas, which he carried through the years to appear before us as a direct, uncompromising, and nonconforming individual stating his opinions irrespective of authority figures. Wedensky was a disciple of Sechenov but diverged from his tutor; likewise Beritoff disagreed with his own professor, Wedensky (Grigoryan, 1986).

In spite of somewhat complicated interrelations between the master and the apprentice, Beritashvili always appreciated the important role of Wedensky in his maturation as a scientist, and for the professor's support of his experimental research as a young scholar. Afterwards, in his memoirs in 1969, Beritashvili wrote: "In my life I had some serious critical moments while working at the Wedensky's lab, however they all worked in my favor" (Beritashvili, 1991, p. 38).

As if correcting the previous mistake about his degree, the St. Petersburg (Leningrad) University awarded Beritashvili the academic doctoral degree (Honoris Causa) on the occasion of his 50th birthday and 25th scientific activity anniversaries in 1935.

Homecoming: Foundation of National School of Physiology and Neuroscience

Not yet being aware that he would spend the major part of his life in the homeland, Beritoff worked for the four years from autumn 1915 to autumn 1919 in Odessa at Novorossyisk University. As a private docent without an academic degree he gave the lectures and worked very hard in the laboratory. In spite of a very complicated situation caused by the civil war in Russia, Beritoff carried out experiments on conditioned reflexes in dogs and pigeons. He also studied the effects of strychnine poisoning on the cerebral cortex of dogs.

But the most important event in Odessa was Beritoff's meeting Olga Antonovna Nivinskaya, who was his student, and after two years of courtship this young pretty girl became his wife. In September 1919 the newly married couple departed to Georgia by ship.

Having had preliminary negotiations with the founders of Tiflis University, Beritashvili began the teaching course, with experimental demonstrations, and work in the research laboratory of the Department of Physiology in autumn 1919. Here, in his native land he laid a strong foundation for the Georgian national school of physiology and neuroscience, the scientific traditions and practice of which are continued by the sixth generation of Georgian investigators.

The idea of establishing a research institute occurred to Beritashvili in the 1920s but required firm governmental support for its work. Initially, and for ideological considerations or protection, he proposed an Institute of Physiology of Labor, similar to numerous institutes operating in big cities of the Soviet Union. At last, in 1934 Beritashvili set up the Institute of Experimental Biology, which was renamed the Institute of Physiology of Tbilisi State University in 1935.

Prior to 1930, the Medical Institute, now the State Medical University of Tbilsi, in which the Chair of Physiology was organized with support from Beritashvili, was an independent institute separate from the university. The first head and Chair was Prof. G. S. Vatsadze, who graduated from the Medical Department of Moscow University in 1916, and then A. N. Bakuradze, one of the close disciples and friends of Beritashvili. The department's research interests were concentrated on many aspects of general physiology, but in particular on digestion and regulation of gastrointestinal function, respiration, energy balance, metabolism and nutrition, and endocrine functions.

Unlike at the Medical Institute, the fundamental investigations at both the Department of Physiology and the Institute of Physiology of the University were focused on the study of Central Nervous System (CNS) problems. At the same time, other and no less important questions about the peripheral nervous system were being investigated. In 1938–1939 a cathode ray oscilloscope replaced the string galvanometer. Beritashvili had become one of the first to employ oscilloscopic techniques in the Soviet Union, and he also extensively used the newly introduced Horsley-Clarke stereotaxic apparatus and conducted EEG Studies.

Actually, after becoming a part of the Georgian Academy of Sciences in 1941, the Institute of Physiology grew into one of the chief centers of neuroscience in the USSR, occupying the third position after St. Petersburg and Moscow.

One of Beritashvili's peculiar features as a representative of the Russian physiological school was his wide multi- and interdisciplinary approach to nervous system research. That is why he always supported and continued to establish new departments in the institute, especially those of the Pathophysiology of the Nervous System (V.V. Voronin), Biochemistry (P.A. Kometiani), Neuromorphology (A.D. Zurabashvili), Biophysics (M.M. Zaalishvili), and Radiobiology (G.S. Vatsadze).

Figure 3. A group of participants at the 15th International Physiological Congress in Moscow (1935). Front row: I. Pavlov, the second and I. Beritashvili, the fourth on the left; the second row: A. Ukhtomsky just behind Beritashvili.

Later, there emerged laboratories for the study of cerebral blood circulation (G.I. Mchedlishvili), electron microscopy (A.L. Mikeladze), membrane biophysics and biochemistry (Z.P. Kometiani), neurocytology (I.K. Svanidze), nervous system development (T.D. Javrishvili), brain metabolism (N.P. Mitagvaria), neurochemistry (D.G. Mikeladze), neuropharmacology (V.N. Chikvaidze), and neuroendocrinology (E.S. Moniava). This list clearly emphasizes the great variety of biomedical sciences involved into the study of nervous system.

Traditional topics of basic and systems neurophysiology were also investigated, among them: sensory systems and receptors (N.N. Dzidzishvili), hearing and vestibular processes (S.N. Khechinashvili), cerebral cortex (A.I. Roitbak), brainstem structures and reticular formation (S.P. Narikashvili), motivation and emotion (L.R. Tskipuridze), electrical activity of the cortex (D.M. Gedevanishvili), conditioned reflexes in monkeys (A.N. Bakuradze), animal behavior (M.M. Khananashvili), hemispheric specialization and interaction (V.M. Mosidze), basal ganglia, and problems of pain (S.M. Butkhuzi), and the cerebellum (G.L. Bekaia). The topics currently being investigated in the institute cover a number of modern and exciting developments.[2]

[2]At present, many of the exciting problems of recent neuroscience are being investigated: the sleep-wakefulness cycle (T.N. Oniani), spatial learning and memory (T.L. Naneishvili), associative memory in the limbic system (L.R. Kvirkvelia), mechanisms of inhibition in cortical neurons (T.S. Labakhua), non-opioid analgesia in pain states (M.G. Tsagareli), brain asymmetry and handedness (M.A. Makashvili), the thalamo-cortical relations (Z.I. Nanobashvili), psychophysiology of stress (V.I. Maloletnev), neurons and glia ultrastructure (I.L. Lazrishvili) and of histochemical studies (M.G. Zhvania), pharmacology of emotions (A.G. Koreli), the visual system (A.R. Kezeli), molecular aspects of imprinting (R.O. Solomonia), molecular genetics of behavior (F.A. Kalandarishvili), and finally, the biophysics of blood flow and vessels (V.A. Mamisashvili). In the middle of the 1980s two independent research institutions were separated from the Institute of Physiology — the Institute of Biophysics and Molecular Biology (T.M. Zaalishvili) and the Institute of Radiobiology (K.Sh. Nadareishvili).

"Gagra Talks" and Establishing IBRO

After World War II, Beritashvili decided to arrange meetings in the style of symposia, in which participants would not be restricted in the time given them to discuss their work. It is well known that at ordinary conferences there is shortage of time for both detailed reports and discussions. Beritashvili planned to limit the number of participants (15–20), but not the time for oral presentations and discussions (Dzidzishvili, 1978).

According to the famous historian of neuroscience, Louisa H. Marshall (1996), a sequence of events on both sides of the Atlantic led to four pioneering series of conferences, each in a different country, among them Beritashvili's symposium, later well-known as "Gagrskie Besedi" ("Gagra Talks"), that fueled the organization of IBRO.

Ivane Beritashvili initiated a third program in this pattern in 1948 and between 1948 and 1972 under the auspices of the Georgian Academy of Sciences, six conferences were mounted in the neurobehavioral sciences with participants drawn chiefly from the Soviet Union. The symposia took place in Gagra, one of the most picturesque resorts on the Black Sea coast in the west region of Georgia. A two-week stay in the balmy January climate seemed to appeal to scientists from the blustery winters of northern and central Russia, because attendance at the Gagra conferences virtually doubled during the series, from 17 in 1948, to 33 in 1972. Beritashvili's unique leadership encouraged younger Soviet scientists by giving them the opportunity of presenting papers and meeting senior scientists in their fields. The third Gagra symposium, on the formation of temporary nervous connections in conditioned reflexes, was held only a few months before the exciting Moscow Colloquium in 1958. One of the United States's participants, Frank Morrell, was a young attendee who had been invited to this Gagra Conference because of his discovery of mirror EEG foci (Marshall, 1996). It is interesting that of the 21 participants at the Gagra Symposium, 15 attended the Moscow Colloquium, so that Gagra served as a preparatory workshop or seminar for the Moscow meeting (Magoun, 1991).

The four series of conferences in as many different countries — the Macy in New York (the last five organized by Horace W. Magoun in 1958–1960), the Ciba in London (commencing in 1950), Marseille (the first in 1950 organized by Henri Gastaut), and Gagra — were indicative of the wide interest in brain and behavior research that was just entering its ascendancy. These events were promoted to found an international organization for the study of the nervous system, IBRO, and later the Society for Neuroscience (Marshall, 1996).

The birth of IBRO followed directly from a resolution formulated at the end of the important International Colloquium on the subject of "Electroencephalography of Higher Nervous Activity" held in Moscow, October 6–11, 1958. It resulted from the first cooperation between Western and "Soviet" physiologists after the end of the Stalin era and the iron curtain had been dispensed with. After the 15th International Congress of Physiological Sciences in Moscow-Leningrad in 1935, under the Presidency of I. P. Pavlov and with I. S. Beritashvili as vice-president, this 1958 conference was the second great event in the USSR. fortynine delegates from 17 different countries throughout the world, an equal number from the East and West, attended the Moscow Colloquium. The Honorary Presidents were Ivane S. Beritashvili and Herbert H. Jasper. Acting Presidents were Henri Gastaut and Vladimir S. Rusinov. The resolution, signed by Beritashvili, Jasper, Gastaut, and Rusinov, and passed by a unanimous vote of Colloquium delegates may be considered the foundation of IBRO (Jasper, 1991).

After the conference, and not only while staying in Moscow, the active participants were guests of the Academy of Sciences of the USSR on trips to Leningrad, Kiev, and

Figure 4. The participants of the first Gagra symposium (1948). I. Beritashvili, in the center, the fourth on the left.

Tbilisi where they visited tourist sites as well as the many laboratories in which the most active brain research was being carried out. These included the Pavlov Laboratories and Institute in Leningrad, the Institute of Physiology in Kiev, and Beritashvili's Institute in Tbilisi (Jasper, 1991). The capital of Georgia welcomed Jasper, Magoun, Brazier, and Robert Galambos. The visitors showed lively interest in all the research activity of the institute and talked to many Fellows about mutually exciting problems. The guests were so delighted with what they saw and experienced during the brief periods of spare time, which even allowed them to make good friends with numerous Georgian scientists, that they then felt sad about leaving Tbilisi. The more so, in that they had become desirable visitors to the homes of their Georgian colleagues (Dzidzishvili, 1978).

Many other famous physiologists later visited the Institute of Physiology in Tbilisi, among them the two Nobel laureates R. Granit and B. Katz, and also W. R. Adey, T. H. Bullock, R. W. Doty Sr., H. Gastaut, H. E. Huxley, K. Lissak, W. J. H. Nauta.

Beritashvili's Legacy: Neurophysiology

As mentioned above, on the basis of experiments with local strychninization of the spinal cord in frogs, Beritashvili determined in 1910 that the coordinating apparatus for flexure reflexes is located in the dorsal horn of the segment where the sensory fibers of the corresponding receptive field entered. It was his first work, 40 years later, with the same experimental design but using the oscilloscope and registration of electrical potentials of the sensory and motor roots, he confirmed the correctness of the principles he had formulated earlier. In particular he showed in 1950 that even when poisoned with strychnine, intercalary or internuncial neurons ("interneurones") of one segment excited through the

appropriate dorsal root fibers activated motor neurons in the given segment but without involving the existing interneurons (Beritashvili, 1975).

Central Coordination of Spinal Reflexes

In Wedensky's laboratory, and at the same time as Sherrington, Beritashvili used the string galvanometer to study the central coordination of spinal reflexes in the registration of action currents of antagonist muscles. In 1913–1914 he discovered the rhythmic nature of reciprocal inhibition. On this occasion Prof. A. A. Ukhtomsky, the second figure in Wedensky's laboratory, and renowned as the author of the "Principle of the Dominant" of functioning in spinal and brain neural centers, said that "for this discovery the young Beritoff achieved his own fame in the history of European physiology" (cited by Grigoryan, 1986, p. 12). Ten years later, in 1924, E. D. Adrian, J. F. Fulton, and E. T. Liddell (1924) confirmed these findings.

At the end of the 1940s Beritashvili with his disciple A. I. Roitbak investigated spinal reflexes in strychninization, again using the oscilloscope. They revealed that the rapid decrease of motor root electrical potentials to high frequency stimulation is caused by the refractory period (15–20 msec) of the interneurons (Beritashvili, 1975).

As early as 1912 Ukhtomsky proposed that Beritashvili should study reciprocal excitation and inhibition in cats and two years later they resumed work on tonic reflexes and electric potentials of muscle in decerebrated cats. After returning from working with Magnus, Beritashvili renewed his experiments on cervical and labyrinthine tonic reflexes with even more success. He showed that during the rotation of the neck around the body in which the receptors of the neck muscles were stimulated, and during changes of head position, in which labyrinthine receptors were stimulated, the only effect was an increase of excitability of certain tonic centers. By 1915 he concluded that the tonic reflex appeared to be due to excitation of these tonic centers in response to additional peripheral stimulation. R. Magnus included these data in his famous book *Körperstellung* of 1924.

While studying tonic reflexes in 1937 using the effects of local poisoning of the spinal cord and cerebral cortex, and changing the parameters of stimulation and duration of mixed (sensory and motor) nerve fibers, Beritashvili found the key to the complicated phenomena of the dynamics and variability of reflex activity. In the presence of an abnormally high excitation center, the neurons located in that area are excited by the impulses irradiating from other CNS sites (Beritashvili, 1984).

General Inhibition

Beritashvili was greatly interested in the problems of general inhibition. Together with collaborators he showed that this phenomenon, first discovered by I. M. Sechenov in 1863, could be induced by the stimulation of the skin, the sensory and autonomic nerves, the visceral organs, and the surface of the brain. The investigation over the period 1928–1943 of such complicated states as eating in dogs and the cutaneous stimulation of the head in frogs and dogs showed that, together with certain motor reactions, general inhibition took place. Beritashvili concluded that general inhibition was an indispensable component of CNS response to any stimulation, even subthreshold stimulation that evoked an outward reaction. The biological significance of general inhibition consists in the fact that: (1) in response to stimuli important for life, excitation is restricted to the nerve centers responsible for the appropriate outward reaction; (2) under weak stimulation, general inhibition protects the organism from the wasteful expenditure of energy.

In 1936–1937 Beritashvili arrived at the very interesting conclusion that general inhibition was a function of what he called the "neuropil" of the brainstem that not only exerted general inhibition but also general excitation on the CNS. What Beritashvili called the neuropil is the structure, which is now well known as the reticular formation. Sadly, his four papers on this problem were published only in Soviet journals and the world physiological community did not pay them proper attention. In 1949 H. Magoun and G. Moruzzi discovered and described this phenomenon precisely.

While studying single reflex contractions of muscles in cats in 1941, Beritashvili demonstrated, independently of B. Renshow, the antidromic inhibitory effect. Moreover, he showed that antidromic inhibition extends through several segments and even both sides of the spinal cord.

Beritashvili was one of the first physiologists to appreciate fully the role of dendrites and in 1941 formulated the notion that dendrites generate local, nonconductive currents in response to impulses. Now this principle is well proven for apical dendrites of pyramidal neurons.

Beritashvili's Legacy: The Science of Animal Behavior

While studying conditioned reflexes in Tbilisi from the end of the 1920s Beritashvili began to investigate animal behavior. He introduced a new experimental device allowing free movement in animals. In contrast to Pavlov, he declined to use a stand for dogs and observed the behavior of animals (rabbits, cats, dogs, monkeys) during unrestricted locomotion within the experimental space. It was a good and bold decision because it provided more natural conditions for studying acquired reflexes and behavior and, although a peculiar method, through it Beritashvili contributed importantly to the science of animal behavior.

Psychoneural Behavior

In the study of conditioned reflexes by the method of free movements, Beritashvili was confronted with actions that could not be explained by or described as conditioned-reflexes. For instance, if the animal only once found food at a given place, on that and following days it ran to the same place. Beritashvili concluded that in higher vertebrates an *image* of the food and its location arose during the animal's perception of the food. This image was reproduced when the animal was in the same situation; moreover the animal later behaved in the same manner by sniffing, etc., if it returned to the place where it had first found the food. This orientating, or investigatory image-guided behavior, supposed the projection of the image of the object the animal recognized onto the outer environment where it had first perceived the food. Such image-regulated behavior was termed by Beritashvili psychoneural, or image-driven behavior. In 1932–1936 he established the fundamental principles underlying his doctrine: (1) the ability of neuronal ensembles to integrate the outer environmental elements into one whole experience, i.e. the integrated image of the outer world. For this purpose it was enough that the animal perceived a scene only once for that image to be reproduced weeks and months after; (2) the temporary connections between the psychoneural circuits and the cortical and subcortical motor centers started to become integrated, with the consequence that the image-driven behavior was readily automatized; and (3) psychoneural activity determined basic animal behavior, and in certain situations suppressed conditioned- and unconditioned-reflex behavior. On the basis of morphological data, Beritashvili concluded that the star-shaped neurons with

short axons in layers III and IV of the cerebral cortex have a special function in psychoneural activity (Beritashvili, 1969).

Beritashvili first summarized his theory in his *Concerning Basic Forms of Neural and Psychoneural Activity* (Beritov, 1947), which caused some negative reaction from Pavlov's school. Beritashvili's conclusion that the psychoneural activity differed in principle from conditioned reflexes was the particular reason for an eventual dispute among Russian physiologists. According to Beritashvili, compared with the neural basis of conditioned-reflex behavior, the neural substrate of psychoneural behavior was distinguished by a characteristic morphological feature. The class of sensory star-shaped interneurons, also referred to as spiny stellate cells (small multipolar neurons with local dendrites and axonal arborizations), did not provide a necessary link for the closed nervous circuits in classical conditioning. Since the functional system of cortical neurons inducing the image was formed at the time of the first perception, while the conditioned reflex needed repeated reinforcements, Beritashvili presumed that difficulties in the development of conditioned reflexes were associated with the special features of projective pyramidal neurons (Beritashvili, 1965).

This difference of opinion between Beritashvili and the representatives of the Pavlov school provided the basis for classing Beritashvili among the "antiPavlovians." It happened in the summer of 1950, at the joint session of the Academy of Sciences and the Academy of Medical Sciences of the USSR devoted to problems of the physiological concepts and scientific legacy of academician I. P. Pavlov, that Beritashvili together with Professors L. A. Orbeli, P. K. Anokhin, A. D. Speransky, L. S. Stern, N. A. Rozhansky, and other prominent scientists, were declared "enemies of Pavlov's doctrine" (Langue, 1997). It is significant that one of the speakers called Beritashvili an ideological and political enemy of the USSR who demonstrated solidarity with reactionary scientists of the United States America wanting to drop atomic bombs on Soviet cities (Kostandov, 1991). All these events were the result of the politicization of science and the formation of a system of state control over science by untalented "red" communist scientists allied with Communist Party leaders in the USSR.

As a result, Beritashvili was dismissed from the post of Institute Director and deprived of scientific work. He was denied access to the research laboratory and his disciples and collaborators were afraid to come to his home. But Beritashvili could not stand being idle and began to study the development of biological thought in ancient Georgian manuscripts. As was typical of him, he worked very hard in archives and libraries. This period of his life was crowned by the publication of his *The Theory of Human Nature in Ancient Georgia, IV–XIV Centuries* published in Georgian in 1957, and Russian in 1961.

Fortunately, by the period of "thaw" in 1955 after Stalin's death, the Thirteenth All-Union Congress of Physiologists, Biochemists and Pharmacologists and then the Board of Academy of Science of the USSR judged all the resolutions and decisions of the period of 1950–1953 negatively. To a man, the repressed scientists and those once in disgrace were able to begin work again. Beritashvili was again as the Head of the Department of Animal Behavior and Chairman of the Institute Council.

Spatial Orientation

After returning to the institute, Beritashvili focused his research on problems of spatial orientation in higher vertebrates, infants, and man. Spatial orientation in the environment is manifested by the ability to project or to localize the position of an object perceived in the outer environment in relation to oneself and other external objects.

Beritashvili established that some kinds of receptors are involved in imaging spatial orientation, but that only the stimulation of visual, auditory, and labyrinthine receptors can induce images of the spatial arrangement of external objects in the environment and their spatial relations to the animal's location. By subtle experiments he demonstrated that the stimulation of labyrinthine receptors during animal locomotion is very important for spatial orientation in the environment, and that proprioceptive excitation did not participate in the production of the image of the route the animal had travelled. But in repeated traversing of the route the stimulation of these receptors turn into conditional signals for movements that then proceed automatically as chain-conditioned reflexes. Experiments extirpating various cortical regions in dogs and cats demonstrated that the front half of the suprasylvian fissure is responsible for spatial orientation under labyrinthine and auditory stimulation.

In infant ontogenesis spatial images arise first by visual perception, then by vestibular, and finally by auditory perception. Special spatial orientation studies in the blind showed that the latter judged obstacles in the distance by sensations in the face area because of cutaneous receptor stimulation resulting from conditioned-reflex constriction of the face muscles. All these investigations were included in Beritashvili's *Nervous Mechanisms of Spatial Orientation of Mammals*, published in Russian (Beritashvili, 1959).

Study of Emotions

Beritashvili was one of the first researchers in the Soviet Union who investigated, in 1950–1965, the fundamental neurophysiological basis of emotions. By the methods of cortical extirpation and subcortical lesioning, and by electrical stimulation of these structures during free movement he found that the paleocortex is the basic substrate of emotional reactions. It is here that the sensations of pain, starvation, fear, rage arise, and at the same time the neocortex is involved in the regulation of emotional reactions. Furthermore, Beritashvili concluded that the organization of behavior, with its internal emotional sensation and external expression, must occur in the limbic system. The neocortex produces its images by reflecting the outer world, and through a great number of inborn and acquired neural connections it triggers the limbic system mechanisms that adapt the organism to external environmental conditions (Beritashvili, 1975).

Study of Memory

Beritashvili's work in last decade of his life was devoted to research into memory. He distinguished three types of vertebrate memory: image-driven memory, emotional memory, and conditioned-reflex memory. In his experiments, image-driven memory was investigated by the method of delayed responses during free movement. Beritashvili with his collaborators carried out fundamental research on the phylogeny of the memory image and found that, particularly in fish, amphibians and reptiles, only short-term memory images were formed, but that in birds (hens, pigeons) long-term memory images formed as well. In the phylogenetic development from fish to monkey, short-term memory extends from several seconds in fish to some dozens of minutes in higher vertebrates. Long-term memory extends from several minutes in birds to several months in dogs and monkeys. According to Beritashvili, for all vertebrates image-driven memory is a result of forebrain activity; with the development of the cortex, image-driven memory becomes its most

important function. For instance, the associative areas of the proreal fissure and the temporal lobe play a key role in the retention of the images of recognized objects. Beritashvili considered the substrate of image-driven memory to be the neural circuits between the proreal fissure, the visual cortex, the inferior temporal cortex, and the hippocampus (Beritashvili, 1972).

It should be noted here that in the context of the current western framework of various theories of memory, Beritashvili's "image-driven" memory is consistent with such other definitions as "declarative memory" of L. Squire, "explicit memory" of E. Kandel, "internal representation" of P. Goldman-Rakić, and the "cognitive map" of J. O'Keefe (Natishvili, 2000).

Beritashvili also used histological and biochemical methods to explore memory. Side by side with the famous Swedish biochemist H. Hyden, Beritashvili paid attention to the molecular aspects of the problem. On the bases of the data of his collaborator, the biochemist Prof. P. A. Kometiani, Beritashvili suggested that the longer retention of the image-driven memory of the location of food seemed to be dependent upon molecular and submolecular changes of proteins in the activated postsynaptic site of neurons. These newly synthesized proteins acting on the postsynaptic membrane facilitate transmission of

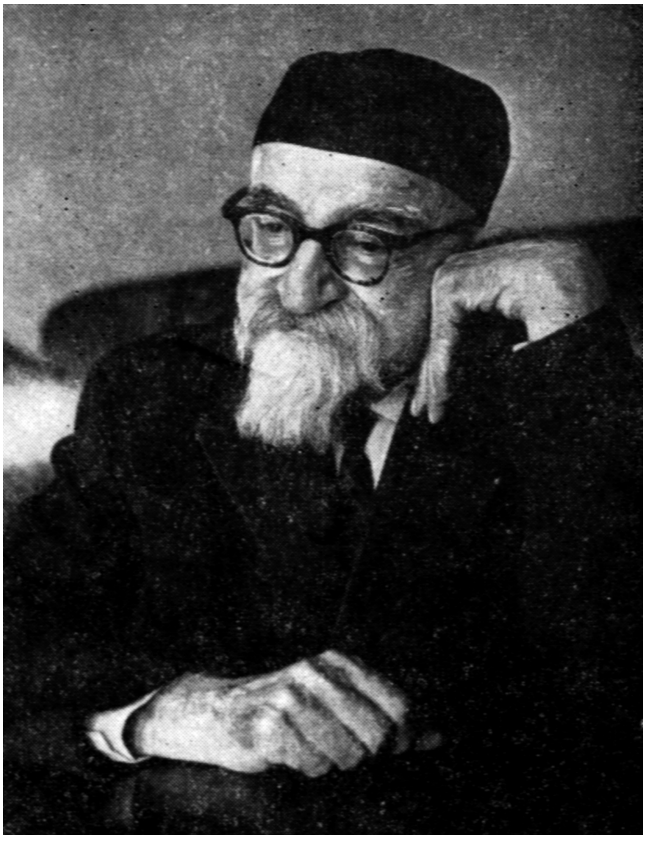

Figure 5. I. Beritashvili, December 18, 1974, just 12 days before his death. In his later years he proudly wore the embroidered black felt skull cap characteristic of the Kakhetian people of the east region of Georgia.

impulses to these sites that could be maintained for days and weeks thereby providing conditions for long-term memory (Beritashvili, 1974).

Beritashvili's book on memory problems, *Memory, its Characteristic and Origin in Vertebrates*, was first published in Russian in Tbilisi in 1968 and translated into English with W. T. Liberson as Editor and published by Plenum Press (Beritashvili, 1971). The second revised and enlarged edition was published in Moscow (Beritashvili, 1974) not long before his death.

Concerning Beritashvili's doctrine of image-driven memory, I wish to cite the eminent Canadian psychologist Donald O. Hebb: "It gives me great pleasure to pay tribute to extensive and fundamentally important work of Professor Beritashvili in the study of physiology and psychology of behavior. As part of this work he has shown the significance of the conception of the image in the analysis and understanding of animal behavior. Obviously this applies also to man's behavior, and indeed with even greater force" (Hebb, 1975, p. 64).

In the last years of his life Beritashvili proposed that the basis of the rational activity underlying the complicated goal-directed behavior of animals was the images of the environment retained in memory, and that animals planned the ways of achieving their own goals.

Concluding Remarks

The results of almost 70 years of original experimental and theoretical work by Ivane S. Beritashvili, which started with his investigation of simple forms of spinal reflexes and nerve-muscle preparations and ended with his study of complicated image-driven memory and animal psychoneural behavior, made a monumental contribution to neuroscience. The phenomena that he discovered and the hypotheses he advanced are the sources for further elaboration of many problems of modern neurophysiology and neuropsychology. Beritashvili's work also reflects not only his search for neural and cerebral mechanisms, but his courage, patriotism, and infinite faithfulness to science, scientific ideas, and principles and traditions, as well as his personal honesty and sense of justice.[3]

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[3]Interested readers can see the list of publications of I. S. Beritashvili in German, English, and French at the end of Doty's paper dedicated to him (Doty, 1975), and Beritashvili's annual review of physiology article (Beritashvili, 1966) as a simple guide to his methods and theoretical ideas to that date.

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