I.S. Beritashvili and Psychoneural Integration of Behavior

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Abstract. Ivane S. Beritashvili's doctrine of psychoneural or goal-directed behavior was established in the late 1920s. It bears a strong resemblance to the concepts of purposive behavior and "cognitive maps" developed in parallel by Edward C. Tolman (1932), and significantly anticipated respective modern concepts. Beritashvili's research was motivated by a disagreement with Ivan P. Pavlov concerning the physiological bases of conditioned reflex formation. In the late 1920s, Beritashvili came to the conclusion that due to the great restrictions it placed on animals' behavioral repertoire, the Pavlov-Bechterev type of conditioning was not a proper model for the study of behavior. Instead, Beritashvili came to prefer the method of "free movement" of the experimental animal. He then pursued an ingenious and extensive investigation of comparative memory in vertebrates. This revealed the unique nature of mammalian memory processes, which he forthrightly called "image-driven" and unequivocally distinguished from memory processes underlying conditional reflexes. These extraordinary works led to the discovery of the mediation of animal goal-directed behavior by image-driven memory.

Keywords: animal behavioral science, conditioned reflexes, goal-directed behavior, image-driven memory, learning, spatial orientation

1 Introduction

The phrase *"psychoneural integration of behavior"* was used by Ivane S. Beritashvili[†] in the title of his article in the Annual Review of Physiology in 1966 [1], which formed the prefatory chapter to a thick volume covering numerous areas of physiology. To some degree following Ivan M. Sechenov [2,3,4], Beritashvili at first referred to "psycho-neural activity" in his explorations of feeding behavior in dogs, and to the method used in his studies as that of "free movements". 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. He was the founder of the national school of physiology and neuroscience in Georgia. In 1958–1960 together with Herbert Jasper, Henri Gastaut, he was one of the founders of the International Brain Research Organization (IBRO).

Ivan P. Pavlov, Vladimir M. Bechterev, and I.S. Beritashvili studied conditioned reflexes mainly with regard to one aspect of animal behavior: salivary secretion in feeding and/or defensive flexion of the paw. Theoretical propositions obtained this way could be only very tentatively extended to whole behavior, as the whole act of adaptation to the environment [1,5]. This fact prompted Beritashvili, in 1928, to start studying feeding behavior by the method of free movements. Later, he exchanged the term "psychoneural activity" for "image-driven behavior". As outlined in his two famous books [6,7] (translated into English with the support of Herbert W. Jasper), Beritashvili meticulously studied this phenomenon for some 40 years, investigating the influence of various sensory factors on the retention of the "image" of food (or punishment) and its location [8]. An extensive series of experiments on fish, amphibians, reptiles, birds, cats, dogs, and primates allowed him to define the phylogenetic and ontogenetic development of this behavioral capability, and to conclude that it is exclusively a function of the forebrain, and especially of the neocortex [9].

Beritashvili took interest in problems of memory since the early 1930s. His major contribution to the science of animal behavior was the demonstration of the universality of learning following a single presentation of an object vitally important to the animal: either a food object or a noxious agent. He postulated that following a single presentation of such objects, an image may be formed of them in the brain, and thereafter the behavior of the animal proceeds as if it actually saw the represented object [7]. Beritashvili showed that such "image-driven" behavior has a strong spatial component, i.e., the image is projected into a definite point in space. This observation led him to devote years of work to problems of spatial perception and orientation [10]. Thus, Beritashvili and his numerous associates

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came to maintain that, in addition to Pavlovian learning by conditioning through repetition of associations, there exists a class of behavior that is *image-driven* and does not require such repetition. Applying different experimental procedures, they showed that these two distinct modes of learning are supported by different functional processes and anatomical structures [5,7]. Furthermore, the difference of "image-driven memory" and "conditioned memory" concerns not only the number of repetitions, but also and above all the ability of the brain to repeatedly reproduce images of the outside world, based on a mechanism for generating percepts from within [11]. What is entailed by the "image" refers to anticipation, expectancy of events to come, and such anticipatory processes may be argued to form the very essence of brain activity. To be able to maintain in the brain all relevant "images" of the animal's world and to process their interactions constitutes the essential meaning of higher forms of brain activity.

Most importantly: from this viewpoint, the difference between the memory resulting from a single presentation of an object and the memory related to an object's repeated perception may only reflect a difference in their respective *modes of repetition*. A single presentation of an object may be followed by multiple reproductions of its "images" in the brain of a motivated animal, and thus, in the final analysis of both cases, memory depends on the repetition of perceptions – reinforced either by an unconditioned stimulus or its images.

2 Beritashvili and the Concept of "Individually Acquired" Reflexes

During the "Odessa period" (1915-1919) of his work, Beritashvili assumed the position of a private-docent in the physiology department of the Novorossiysk University. A major research endeavor of this period was the careful study of "individually-acquired" reflexes according to the Bechterev procedure of defensive reflex formation in dogs. In these studies, Beritashvili registered the motion of extremities and also the respiratory and orientating movements of the head while the animal was tied in a soundproof cabin. Conditioned defensive flexions of the paw in response to sound and photic stimuli were developed by combining that latter with painful electrical skin stimulation. This work appeared in 1924 as two papers [12,13], which were some of the first publications on conditional reflexes in English, and appeared then in German (1927) [14], and finally as a comprehensive monograph in Russian (1932) [15]. The same monograph summarized the research of Beritashvili's laboratories in Odessa and Tbilisi since the preparation of his first book on reciprocal innervations of skeletal musculature (1916) [16]. In his second book, Beritashvili reviewed a wide range of pertinent literature on Pavlovian conditioning from all Russian laboratories and provided a vivid description of his own approach of "individually-acquired" reflexes.

In the preface to this voluminous work, Beritashvili for the first time gave a definition of animal behavior. He clearly distinguished the concepts of conditioned reflexes and whole animal behavior. According to him, there are three distinct forms of behavior in invertebrates and vertebrates. The lowest form of behavior is innate and entirely dependent on the genetic organization of the central nervous system (CNS). This form of behavior is typical for all invertebrates and lower vertebrates like fish and amphibians. Further in phylogenetic development, a new type of behavior develops based on conditional learning in ontogenesis and earlier innate behavior. This behavior plays a powerful role in higher vertebrates – birds and mammals. Finally, the highest level of behavior is reflected in the psychoneural or goal-directed behavior. This form of behavior is aimed at achieving final, already known goals in various ways based on their images [15].

Beritashvili emphasized that unlike a reflex, the whole behavior has no receptive field. Behavior is determined, on the one hand, by the effect exerted by almost the entire external environment on the body, and on the other hand, by the internal state of the organism, which is a consequence of the organism's entire previous activity. Thus, according to Beritashvili, the subject of behavioral science is not the study of reflexes, or of isolated reactions of an organ or a complex of organs, but rather the activities of the whole body. Reflexes are only elements that induce whole behaviors; these in turn represent united actions of adaptation of the whole organism to the environment [15]. At the end of the mentioned preface Beritashvili concluded:

"The science of behavior is a special independent science with its own specific principles. It can be defined neither as the general physiology of the CNS, nor through the Pavlovian concept of higher nervous activity, nor through my doctrine of individually acquired activities. However, behavioral science naturally considers all data on the physiology of the CNS, particularly pertaining to individually acquired activities – behavioral acts realized by neural mechanisms of innate and individual activities." [15, p. X].

Between 1933-1935, Beritashvili published 10 reports on dog behavior in the Sechenov Physiological Journal, the editor-in-chief of which was then Pavlov. In these papers, Beritashvili gave the most complete summary of his experimental findings and attempted to lay the foundation for his theoretical concepts [17]. It is important to note that at the beginning of his work on conditioned reflexes and animal behavior more widely, Beritashvili still adhered to the behaviorist view that complex animal behavior is, although holistically organized, only the summation of consecutive unconditioned and conditioned reflexes [18].

3 Beritashvili and the Concept of Image-Driven Behavior

Beritashvili began to investigate animal behavior while studying conditioned reflexes in Tbilisi in the 1920s. He introduced a new experimental approach allowing the free movement of 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, which provided more natural conditions for the study of acquired reflexes and behavior. Through this peculiar method, Beritashvili made an important contribution to the science of animal behavior [19-21].

3.1 Free Behavior

Early on in the Tbilisi period (1919-1941), Beritashvili grew dissatisfied with the unnatural restraints that the conditioning procedure imposes on the animal, and went on to develop a paradigm of "free behavior" in most of his subsequent work on memory. Among his most important decisions, he abandoned the Pavlov/Bekhterev paradigm for the study of conditional reflexes. He was highly critical of this approach [12,13], as well as of the "brainless" psychology (behaviorism) prevalent in North America at that time [14]. Instead, he was attracted by the common knowledge of the ability of dogs to find their way to food, and the brief experiments of Wolfgang Köhler testing this ability in dogs as well as in chimpanzees [22,23]. However, unsatisfied with Köhler's few observations, as well as with Pavlov's explanation of them as examples of conditional reflexes, Beritashvili committed himself to testing behavior in freely moving animals – a method that was inherently natural and versatile. The prototypical example of such learning is that of a hungry dog, brought for the first time into a particular room and fed there at a specific place. Following such a single exposure, the animal would run directly to that place of food immediately upon entering that same room, even if this occurs several months later [20].

3.2 Image-Driven Behavior

Beritashvili straightforwardly called the total feeding behavior of an animal "image-driven", in case its movements during the task were unrestrained. While such descriptive terminology carries some prejudice from the days of behaviorism as being hopelessly anthropomorphic (as it is impossible to *know* what an animal experiences), denying the validity of the term is equally suspect. Given the manifold similarities not only in the anatomy, but also in the psychophysics of many lower primates and man, it is strange to deny that equivalent anatomy and physiology generate similar percepts. Human "image-driven" behavior is itself a sufficiently general experience so that a diminished form thereof seems defensibly lucid in describing the equivalent phenomenon among mammals. In a volume of his selected works, there is an interesting 22-page discussion [24] in fine print between Beritashvili and his Russian colleagues arguing this point and, particularly, Beritasvhili's "modeling" of such behavior as being supported by the spiny stellate cells of layers III and IV of the cortex. He could draw upon the connections revealed not only in the work of Cajal and Lorente de No, but also those of Poliakov and Shkolnik-Yarros to offer appropriate connections based on the Golgi picture [5,6,20].

Beritashvili's method for studying behavior was the following: an animal is habituated to lying quietly in a cage or on wooden shelf in a definite place in a large experimental room (6 × 10 m). Large and small screens stand at a distance of 2 to 8 m from a screened cage where the animal is located (Fig. 1). The animal can not see all of them at the same time because of the way the screens are placed. Usually, the experimenter shows a food dish at a distance of 1.5-2 m within the animal's eyesight then takes it away and lays it behind one of the screens while the animal sees the procedure. After a short time, the experimenter releases the animal from its cage. If it goes immediately and directly to the location of the food, Beritashvili assumed that the feeding behavior is carried out on the basis of an image of this location. After the animal has eaten, the experimenter returns it to its cage. Subsequently, over the course of several minutes, the animal is released for three more times from the cage without reinforcement. The animal initially goes to the same place where it was fed. Then it does not go there or does not even leave the cage. Only after this does the experimenter carry out the next trial, in which food is brought to another location [6,7].

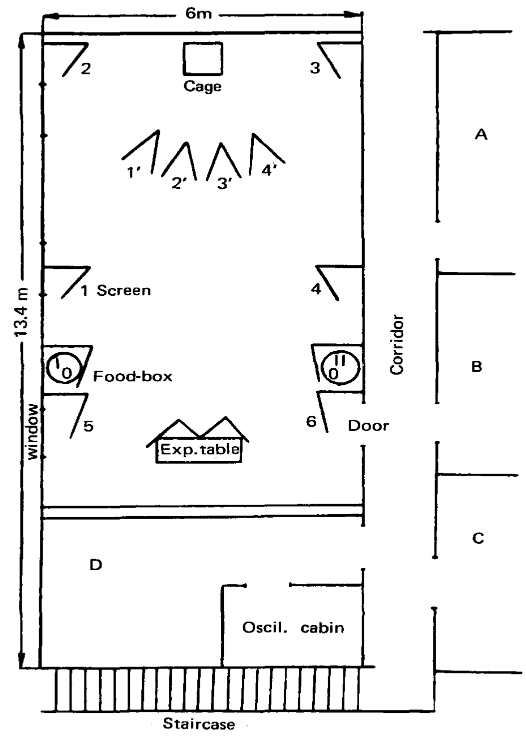

Fig. 1. Experimental arrangement for the study of image-driven behavior using the method of free movement. At the rear wall of the large experimental room stands a cage which is opened and closed automatically. The experimenter's table is in front of the cage at a distance of 6 m, and is enclosed by high screens with slits through which observations on the behavior of the animal are carried out. Small screens in different locations in the experimental room are denoted by 1, 2, 3, 4, 5, and 6, behind which the food is placed. The small screens denoted by 1', 2', 3', and 4', which are in a single visual field at a distance of 1.5 m from the cage, are also used in some experiments. I and II are feeders which automatically open and close, from which the animal feeds during the formation of conditioned feeding behavior. In the study of long-term memory, the animal is first led across the corridor into one of the rooms opposite the experimental room (A, B, C, or D), and is then brought to a particular feeding location [7].

When investigating the behavior of dogs with the described method of free movements, Beritashvili encountered from the very beginning behavioral acts which can by no means be designated as conditional. A hungry animal, fed from a food box only once, is able to run to it without any conditional signal after a minute, an hour, or even a day has lapsed. On the other hand, different combined (conditional) stimuli would cause the animal to run to the food box only after it has been repeatedly fed from it. Or if by chance, a dog or a cat should in the course of its searching movements see food in an unusual place, it would, both on that day and on the following days, run to that place. These and many other data convinced Beritashvili that in dogs as well as in other higher vertebrates, the very first perception of the location of food creates an *image* or a concrete representation of food and its location in the given environment. This image is preserved, and each time it is reproduced in the course of perceiving the environment or any of its components, the animal would perform the same orientating movement of the head and behave similarly to the case of immediate perception; i.e., it runs to the food location, and sniffs and eats the food if it finds it [1].

At first, Beritashvili called such goal-directed behavior *psychonervous,* but then referred to it simply as *image-driven behavior*. He assumed this behavior to be a complex of voluntary movements peculiar to higher vertebrates and mammals as well as to little children. He supposed that whenever a feeding behavior is learned that is directed towards a particular food box, it originally conforms to the reproduced food image. The image of the food-box's location is also reproduced and can play an accessory role [6].

In 1932-1936 Beritashvili established the fundamental principles underlying his doctrine:

(1) Neuronal ensembles are capable of integrating outer environmental elements into one whole experience, i.e., into an integrated image of the outer world. Perceiving a scene only once is sufficient for an animal to reproduce its image weeks and months later.
(2) The neural complex of an image is very easily reproduced under the influence of only one component of the corresponding environment, or a stimulus closely related to the environment.
(3) The neural complex of a given image can be reproduced several days, a week, or even months after its original generation.
(4) Reproducing the image of a vitally important object has an extremely potent driving strength.
(5) In the course of learning, temporary connections between cortical neural circuits and the cortical and subcortical motor centers become integrated, with the consequence that image-driven behavior is readily automatized.
(6) The driving strength of the reproduced image depends on the time elapsed since its generation, the importance of the elements of this image in the animal's life, and the distance separating the animal from the projected goal object.
(7) Image-driven behavior is defined as a basic form of animal behavior, dominating over other types of behavior. It takes precedence over automatized individual behavior and inborn reflex behavior, and suppresses them each time they cease to serve the needs of the organism [6].

On the basis of morphological data, Beritashvili concluded that the stellate (star-shaped) neurons with short axons in layers III and IV of the cerebral cortex have a special function in image-driven behavior. When excited, these stellate sensory neurons produce the elementary subjective sensations of light, color, sound, taste, odor, touch, warmth, and cold. A large number of sensory neurons from one or several primary zones are involved in the perception of external objects. Simultaneously, a multitude of internuncial and association pyramidal neurons are excited in both primary and secondary zones and combine all excited sensory neurons into one functional system. This functionally unified system is fixated, apparently, by means of a more or less firm reorganization of association pyramidal neurons of the secondary zones and association areas. Apparently, upon repeated perception of a portion of a given object or environment in which this object occurs, there is an activation of these same pyramidal and sensory neurons and the same perception is reproduced. This reproduced perception is an image or a concrete representation, e.g., of a feeding scene [5].

In 1947, Beritashvili first summarized his theory in the book *Basic Forms of Neural and Psychoneural Activity* [25], and then extended it in his next monograph *Neural Mechanisms of Higher Vertebrate Behavior* (1961, translated to English in 1965 [6]). Meanwhile, he had studied problems of spatial orientation in mammals in a special book published in 1959 [10]. On the background of the country's difficult political situation, however, the new lines of reseach opened up in these works received negative reactions from the Pavlovian school – particularly after the publication of his 1947 book.

Beritashvili's conclusion that psychoneural activity differed in principle from conditioned reflexes led to a dispute among Russian physiologists, and provided the basis for classifying Beritashvili among the "anti-Pavlovians". Before the death of Stalin and the ensuing abatement of terror, Beritashvili and many of his leading fellow physiologists – L.A. Orbeli, P.K. Anokhin, A.D. Speransky, L.S. Stern, N.A. Rozhansky, and others – were called before the 1950 joint scientific sessions (of the USSR Academy of Sciences and the USSR Academy of Medical Sciences) to confess to being "enemies of the doctrine of Pavlov" [19-21,26].

This atmosphere of terror and repression kept Beritashvili and most Soviet scientists crucially isolated and, in great many instances (Lysenkoism, Pavlov "worship", etc.) hobbled by political restraint. Bravely, Beritashvili followed his own path, and held to a course of highly original experimentation after the period of seclusion from 1950–1955. However, he had to remain sensibly cautious in his Western contacts, being especially vulnerable due to his previous "foreign" publications [20].

3.3 Spatial Orientation

Between 1955 and 1959, after his rehabilitation, Beritashvili focused his research on problems of spatial orientation in higher vertebrates, infants, and man. Spatial orientation in the environment manifests in the ability to project or localize the position of a perceived object in the outer environment in relation to oneself and other external objects. Beritashvili established that various sensory receptors are involved in producing the image of 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. With subtle experiments he demonstrated that the stimulation of labyrinthine receptors during animal locomotion is highly important for spatial orientation in the environment, and that proprioceptive excitation is not involved in producing the image of the route the animal has travelled. However, upon repeated traversal of the route, the stimulation of proprioceptors turns into conditional signals for movements that then proceed automatically like 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 [19,21].

Beritashvili concluded that spatial orientation in higher vertebrates is reflected in their ability to project an object into space and localize its position in relation to oneself or to other objects, and this after a single perception of the respective object by the animal. Also, spatial orientation is required to approach the object or the move from one object to another when the animal neither sees them nor perceives the objects through any other senses. Moreover, all sensory information from receptors may play an important role in spatial orientation. However, the optic receptors and vestibular semicircular canals, utricle and saccule play a most significant part, since their exclusion renders normal orientation in space impossible [1].

In infant ontogenesis spatial images arise first via visual perception, then through vestibular, and finally through auditory perception. Special spatial orientation studies in the blind showed that the latter judged obstacles in the distance by sensations in the face area, based on cutaneous receptor stimulation resulting from conditional reflex constriction of facial muscles. All these investigations were included in Beritashvili's book *Nervous Mechanisms of Spatial Orientation in Mammals*, published in Russian (1959) [10].

3.4 Vestibular System

Beritashvili was acutely aware that image-driven behavior referred not only to an object or event, but also a location. Thus, returning to his early experiments with Rudolf Magnus on the eve of World War I in Utrecht, he performed an extensive analysis of the role of the vestibular system, as opposed to muscular proprioception, in guiding orientation in space [27]. The results were clear, both in cats and dogs, and in children. In the absence of vision, the labyrinthine system, and not muscular proprioception, provides the information necessary for orientation and path registration [20].

Labyrinthectomized animals, even after several months of recovery and specific training, were unable to follow a newly given path when vision was absent (due to blindfolds). With sufficient repetition, they could be trained to pursue a particular path in an unchanging sequence. In other words, they could learn a sequence of turns, but lacking vision as well as the vestibular system, they were wholly disoriented [27]. This has now been fully confirmed with rats [28]. Recent work with human subjects passively translocated through space has suggested that cues other than those provided by the otoliths are important for perceiving features of lateral movement [29]. However, Beritashvili's observations on deaf-mute children definitively demonstrate that in the absence of vision, the labyrinths are essential for orientation and for subsequent following of a path along which these children have been led, or even passively transported. The deaf-mutes lacking labyrinthine function were totally disoriented in this situation, whereas blind children performed significantly better than normal, blindfolded children [27].

3.5 Study of Memory

Beritashvili's work in the last decade of his life was devoted to memory research. Using multiple variations of this theme, Beritashvili studied the mnemonic capabilities of various vertebrates from fish to microcephalic and normal children, the effects of restricted sensory input, and the removal of various portions of the CNS in animals. 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. Together with his collaborators, Beritashvili carried out fundamental research on the phylogeny of image-based memory and found that particularly in fish, amphibians and reptiles, only short-term memory images are formed, whereas in birds (hens, pigeons) also long-term memory images exist. In the phylogenetic development from fish to monkeys, 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, image-driven memory in all vertebrates 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 temporal lobe play a key role in the retention of images of recognized objects. Beritashvili considered the substrate of image-driven memory to be located in the neural circuits between the proreal fissure, the visual cortex, the inferior temporal cortex, and the hippocampus [19].

Summaries of this voluminous work are available in English [7], but are too extensive to be treated here. However, a few notes can be made. First, the phylogenetic series poses several fascinating problems. The evidence is clear that the mammalian neocortex implements a novel process for stabilizing and retaining mnemonic changes in its neural networks, and this process is absent in non-mammalian species. Admittedly, the anadromous behaviors of certain fish and sea turtles do show astonishingly robust retention, and many birds possess remarkable mnemonic ability; yet they lack much of the versatility and retention of momentary events that are commonly displayed by mammals. Beritashvili behaviorally confirmed Herrick's thesis (1927) that the amphibian brain is less advanced than that of fish [30]; and in truncated animals he anticipated Thompson (2005) in focusing on the cerebellum as the site critical for conditional reflexes [31]. In fact, Beritashvili considered conditional reflexes to represent a separate class of memory due to the repetition of paired stimuli required for their establishment. He also studied emotional memory, such as avoidance behavior consequent to an adverse experience, and considered such memories as categorically different from object memories [20].

Although Beritashvili's concept of behavior is markedly different from that of other authors, some of his views can be seen to find close parallels in later work. For example, this holds with regard to the problem of the "situation", as discussed by Wyrwicka [32]. She emphasizes that Beritashvili highlights the role of image memory as a reinforcing agent and its connections with the environment where the reinforcement occurs. By these means, the importance of the situation gains further support even from a remote perspective [32].

On the other hand, in the context of various memory theories in current Western frameworks, Beritashvili's "image-driven memory" is consistent with concepts such as the episodic "declarative memory" of L. Squire, "explicit memory" of E. Kandel, "internal representation" of P. Goldman-Rakič, and the "cognitive map" of J. O'Keefe and Nadel [17].

Beritashvili also used histological and biochemical methods to explore memory. Along with the Swedish biochemist H. Hyden, Beritashvili paid attention to the molecular aspects of the problem. He suggested that longer retention of food location in the image-driven memory may depend on molecular changes in proteins of the activated postsynaptic sites of neurons. These newly synthesized proteins may act on the postsynaptic membrane and facilitate impulse transmission to these sites. By maintaining this facilitation for days and weeks, conditions for long-term memory are provided [11].

Beritashvili's book on memory, *Vertebrate Memory: Its Characteristics and Origin*, was first published in Russian in Tbilisi in 1968 and soon translated into English (1971). The second, revised and enlarged edition was published in Moscow (1974) not long before his death.

4 Modern State of the Problem

A major goal in contemporary cognitive neuroscience is to understand how the brain represents space and how this representation is used to generate behavior. To construct a spatial representation, the brain depends on inputs from our senses, including vision, touch and audition [34].

The debate in cognitive psychology between advocates of stimulus-response theories [35] and cognitive maps [36,37] in the first half of the twentieth century had grounded behaviorally rigorous studies of habitual instrumental control and goal-directed behavior, which in turn provided the foundation for investigating their neural mechanisms [38].

In the early part of the last century, in parallel with Beritashvili, E. Tolman [37] considered a typical learning experiment involving rats negotiating a maze environment to reach a rewarding goal. Tolman argued strongly against what he considered the fundamental poverty of this behaviorst paradigm. Instead, he aligned himself with the so-called "field theorists" [37], who proposed that animals learn this type of maze tasks by forming "a field map of the environment", nowadays more commonly referred to as a cognitive map [37], which provides the necessary guidance mechanism for the observed learning [38].

Cognitive maps occupy a central role in contemporary ideas related to memory and orientation in space [39,40], where the hippocampus has been shown to play a key role [41]. For instance, human subjects with hippocampal lesions manifest a profound impairment in self-projection or prospection when tasked to imagine possible future states [42]. Equally, in rats the expression of "vicarious trial and error" behaviors is abolished by hippocampal lesions [43]. Furthermore, one of the most famous findings about the hippocampal-parahippocampal circuit in rats is the existence of place cells, head-direction cells, and grid cells which provide a population code for representing space [41,44-48]. These studies support Beritashvili's concept of image-driven behavior, but unfortunately they do not cite and virtually ignore his pioneering works.

However, evidence is now accumulating to clothe Beritashvili's image-driven behavior with fact. When a rat is making a choice as to which path it should pursue to find food where it has previously encountered it, the "place cells" in its hippocampus often register the firing pattern seen in the pathway to the goal, rather than that of the location from which the animal is making the choice [50,51]. In other words, the neural activity associated with the remembered path is present to guide the behavior. The visual component per se has not yet been demonstrated to be coupled with that of the pathway to the object, but the existence of neural circuits capable of projecting past events into future action is the very essence of the idea of image-driven behavior. That the hippocampus has a significant role in future actions being guided by past memories is remarkably emphasized by the fact that amnesic patients, with bilateral damage to the hippocampus, are seriously deficient in their ability to conjure up images of imaginary scenes [42], i.e., in their ability to construct images of a similar nature as those called forth in "image-driven" behavior [20].

5 Summary

Beritashvili's works before and after the World War II [10,15,25] on behavior represent a milestone in the history of neuroscience and animal behavior science, particularly given his new ingenious experimental approach to higher brain functions at that time. His subsequent articles and books in English [5-7,9,27] refined his original ideas on the subject, but unfortunately his concept has still not been evaluated properly.

In this respect, we quote Donald O. Hebb, who was aware of Beritashvili's doctrine of image-driven behavior:
"It gives me great pleasure to pay tribute to the 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" [55, p. 64].

6 Briefly on the Life and Times of Beritashvili

Little has been written about Beritashvili in English. For the present purpose of summarizing the key features of his remarkable life and academic career, I have relied primarily on English language sources [8,19,20,26] and some translations from Georgian into English [21].

6.1 Early Life and Training Experiences (1885–1906)

Ivane S. Beritashvili, the son of a priest, was born on 31 December 1884 in the small village of Vegini in Kakheti, in the Eastern region of Georgia (at that time part of the Russian Empire). He studied to become a priest first at the ecclesiastic school in Telavi, the main city of Kakheti, and then at the theological seminary in Tiflis (Tbilisi), the capital of Georgia. However, disencouraged with the prospect of becoming a priest, the young Ivane took his graduation exams at the 2nd Tiflis gymnasium in 1906. In the same year, he matriculated to the Natural Science Division of the Department of Physical and Mathematical Sciences of St. Petersburg University [19-21].

6.2 University Career in St. Petersburg (1906–1915)

Beritashvili began his experimental research early on as a third year student under the supervision of the eminent Russian physiologist Nikolai E. Wedensky. 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 at the Physiological Laboratory of the University [19-21].

On the recommendation of Wedensky, Beritashvili left for Kazan in autumn 1911 to work with Prof. Alexander P. Samoilov to master the method of registering electric currents in nerves and muscles with the string galvanometer. Later, in the spring of 1914, again with Wedensky's support, Beritashvili joined Rudolf Magnus 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 known as the Magnus–de Kleijn reflexes). At the outbreak of World War I, Beritashvili had to terminate his research and return to St. Petersburg [19-21].

6.3 Novorossiysk University in Odessa (1915–1919)

In 1915 Beritashvili had to leave St. Petersburg due to a conflict with Wedensky, and moved to Odessa as a senior assistant to Prof. V.V. Zavyalov at the Department of Physiology in the Physical and Mathematical Faculty of Novorossyisk University [19]. The founder of this department was Ivan M. Sechenov, praised by Pavlov as "the father of Russian physiology", who had headed the department for six years between 1870 and 1876 [3]. Beritashvili would assume the position of a private docent at the same department within a year of his arrival there, and began delivering lecture courses on the physiology of the nerve-muscular system [19-21].

Beritashvili's major endeavor in Odessa was the careful study of "individually acquired" reflexes in dogs by the method of V.M. Bechterev. As noted, however, the limitations of this method soon led him to abandon it for the paradigm of free behavior, developed particularly in his subsequent work on spatial orientation and memory [20].

6.4 Homecoming: Tbilisi University (1919–1941)

The end of the World War I brought an end to the Russian Empire and a brief freedom for Georgia, from 1918 to 1921. An independent government was established in the country, and Beritashvili was installed as the head of the Physiology Department in the newly created Tbilisi University. It must have been an exhilarating time for him, returning to his homeland in September 1919 with his new bride, Olga Nivinskaya, a lovely Russian girl who had been his assistant in the Odessa experiments. He immediately set about writing a textbook of physiology in Georgian that was also translated into Russian, and both texts went through many editions [20]. At the same time, he founded a physiological research laboratory and started intensive work. Beritashvili thus realized what for Ivane R. Tarkhnishvili (Tarchanoff), the Georgian-Russian physiologist who discovered of the psycho-galvanic reflex [56], had been only a dream – to establish a physiological laboratory in his native land [19,21].

In the next decades he would lead a prodigious series of studies in Tbilisi on problems of general inhibition and inborn behaviors; carry out ingenious investigations on interhemispheric mnemonic transfer and comparative analyses of vertebrate memory. Yet, much of this monumental contribution to neuroscience remains untranslated from Russian and Georgian. From 1912 to 1929 he published 42 papers in German and English; however, this was followed by a period of unbroken linguistic isolation for the next 30 years. This hiatus deprived science of a rush of ideas, and caused a loss also for Beritashvili, who was bereft of the enriching exchange with his numerous, like-minded colleagues throughout the world [20].

On the basis of his experimental laboratory at the Tbilisi State University, in 1935 Beritashvili established the research Institute of Physiology which in early 1941 became affiliated with the newly founded Georgian Academy of Sciences. Very soon, the Institute grew into one of the leading centers of physiology in the USSR, occupying the third position after St. Petersburg and Moscow.

Fig. 2. Ivane S. Beritashvili (1884-1974)

6.5 Institute of Physiology[‡] and International Activity (1941–1974)

For more than 30 subsequent years at the Institute of Physiology, Ivane Beritashvili expanded his research into related areas such biochemistry, biophysics, and neuroanatomy to study higher brain functions and behavior, and laid the foundations for Georgian national schools of physiology and neuroscience, their research traditions and practice.

After World War II, Beritashvili arranged meetings in the form of symposia, later well known as "Gagrskie Besedi" ("Gagra Talks") that with conferences on both sides of the Atlantic (by Horace W. Magoun and Henri Gastaut) fueled the organization of the International Brain Research Organization (IBRO). Between 1948 and 1972, under the auspices of the Georgian Academy of Sciences six conferences were dedicated to the neurobehavioral sciences with participants drawn mainly from the leading physiologists of the Soviet Union [57].

The birth of IBRO followed directly from the resolution formulated at the end of an important International Colloquium on the 'Electroencephalography of Higher Nervous Activity' held in Moscow (1958). The Honorary Presidents of this colloquium were I.S. Beritashvili and H.H. Jasper, and its Acting Presidents were H. Gastaut and V.S. Rusinov [57-59].

Ivane Beritashvili died of acute pneumonia on December 29, 1974. He was buried in the square of Tbilisi State University, alongside other founders of the University.

The results of almost 70 years of Ivane S. Beritashvili's original experimental and theoretical work, 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 goal-directed 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 [19,21].

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[‡] Institute of Physiology, which since its foundation bore the name of Beritashvili, was renamed as the Beritashvili Center for Experimental Biomedicine in 2011.

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