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Pioneering Studies of Spatial Behavior in Animals: Ivane Beritashvili and Edward Tolman

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Ivane S. Beritashvili's doctrine of image-driven behavior was established in the late 1920s and finally extended in his books in English (1965; 1971). It bears a strong resemblance to the concepts of purposive behavior and "cognitive maps" developed in parallel by Edward C. Tolman (1932; 1948) and significantly anticipated respective modern concepts. John O'Keefe and his disciples May-Britt Moser and Edvard I. Moser received the Nobel Prize in 2014 for their discoveries of cells that constitute a navigation system in the brain. The latter fact brings us to the pioneers of the study of the spatial orientation of animals that figuratively speaking, provided the giant's shoulders on which O'Keefe and the Mosers stood to receive their award. Beritashvili and Tolman upheld the holistic and goal-directed nature of spatial behavior. A major contribution of Beritashvili 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 signal. Beritashvili showed that such "image-driven" behavior has a strong spatial component, i.e., the image is projected into a definite point in space. Thus, he came to maintain that there is a class of behavior that is image-driven that does not require a repetition of associations. Tolman made several significant contributions to the field of experimental psychology. He thought of learning as developing from bits of knowledge and cognitions about the environment and how the organism relates to it. He examined the role that reinforcement plays in the way that rats learn their way through complex mazes. These experiments eventually led to the theory of latent learning which describes learning that occurs in the absence of an obvious reward. Tolman also strongly advocated the theory that rats learn the place where they have been rewarded rather than the particular movements required to get there. To a great extent, Tolman's work determined the direction of American psychology in the 1930s-1950s. The contribution of Beritashvili and Tolman, thus, is the groundwork of modern studies of spatial cognitive processes in human and nonhuman animals.

Keywords: animal behavior, cognition, conditional reflexes, learning, memory, spatial orientation, navigation

Introduction

In the early 1930s, Ivane S. Beritashvili[1] (1884-1974) and Edward C. Tolman (1886-1959) almost simultaneously endowed animals with the ability to form a neural representation of the external world and use this representation to control behavior. I. S. Beritashvili (Figure 1), whose contributions to physiology of the

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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 on the Russian, German, French, and English publications and sources, respectively.

nervous system started in 1911, has been working in all fields of this science, what we now refer to as neuroscience, from nerve fibers and the spinal cord to the highest levels of brain functions (Beritashvili, 1966; 1971). However, his major contribution has been the demonstration of the universality of learning following a single presentation of an object vitally important to an animal, whether it is a food object or a nociceptive agent. He postulated that following a single such presentation, an "image" of this object may be formed in the brain of an animal, and, thereafter, behavior proceeds as if the animal actually saw the object. Beritashvili showed that such "image-driven" behavior has a strong spatial component, i.e. the image is projected into a definite point in space (Beritashvili, 1971). This observation led Beritashvili to devote many years of his scientific work to the problems of spatial orientation and navigation (Beritashvili, 1965; 1971). Thus, Beritashvili maintained that in addition to Pavlovian learning by conditioning involving repetition of association, there is image-driven behavior which does not necessitate such repetition. He and his numerous associates showed that, by applying various experimental procedures, one may reveal that these two different modes of learning are supported by different functional processes and anatomical structures (Beritashvili, 1971).

Figure 1. Ivane S. Beritashvili (1884-1974) in the middle of 1950s. He established a Department of Physiology (1919) and then a Research Institute of Physiology (1935) at Tbilisi University. In 1958-1960 together with Herbert Jasper (1906-1999), Henri Gastaut (1915-1995), Alfred Fessard (1900-1982), he was one of the founders of the International Brain Research Organization (IBRO).

By the other approach, Tolman asserted that animal learns the correct route through the maze, i.e., a sequence of responses to stimuli appearing at different points of the maze, usually represented by a succession of left and right turns. This "sequence of responses" view suggested that animal can solve the problem correctly because it has a cognitive map of the maze and can use it for finding the way to the goal from any point of the maze.

In contrast to the orthodox behaviorists, Tolman—in line with the theories of Gestalt psychology—upheld the holistic and goal-directed nature of behavior. He was a proponent of the structural-functional rather than the association's analytical method, holding that individual parts of an action are determined by their function within the whole. In elaborating these ideas, Tolman developed his cognitive theory of learning and investigated the phenomenon of "latent learning". To a great extent, Tolman's work determined the direction of American psychology in the 1930s-1950s.

Beritashvili's Doctrine of "Image-Driven Behavior"

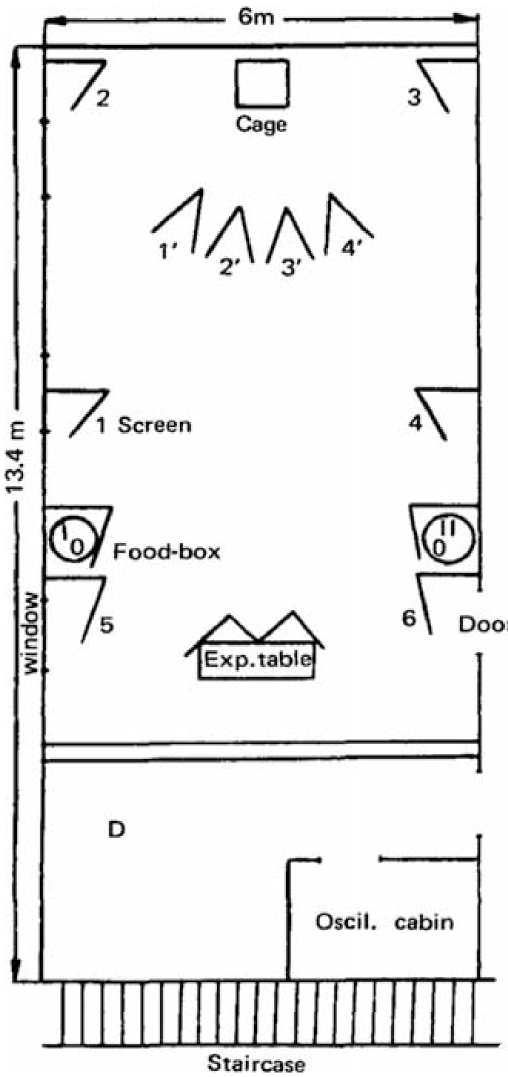

Figure 2. Experimental arrangement for the study of image-driven behavior using the method of free movement. At the rear wall of the large experimental room stands a cage which is opened and closed automatically. The experimenter's table is in front of the cage at a distance of 6 m, and is enclosed by 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 (Beritashvili, 1971).

In the late 1920s, Beritashvili started investigations on conditioned reflexes by Pavlov and Bechterev. He introduced a new experimental approach allowing the "free movement" of animals in large experimental space (Figure 2). Beritashvili's doctrine of image-driven behavior presented challenging blueprints of the organization of structures supporting higher brain functions. Beritashvili posed and attempted to answer different questions from those discussed in his Russian (1932; 1947; 1959; 1968; 1974) and English (1965; 1971) monographs. For instance, if learning is the basis of behavior and memory, how does image-driven memory differ when it is established on image formation following a single association from that which is rooted in conditioning processes requiring many associations (conditioned memory)? How do these memories differ when the animal has a rewarding experience? Which are the structures and functions underlying each of these memories? How are these processes related to the modern concept of short-term and long-term memories, the latter allegedly rooted in the process of formation of highly specialized active proteins? Most importantly, how do these two kinds of memories express themselves in phylogeny from fish to humans, and in ontogeny during post-embryonic development (Beritashvili, 1971)?

Beritashvili and his co-workers carried out a succession of experiments which revealed a monumental body of findings. For example, to the notion of the primary role played by the hippocampus in memory function, Beritashvili opposed the priority of the proreal gyrus in dogs and prefrontal cortex in baboons, at least as far as image-driven memory was concerned. In lower animals conditioned memory did not depend on the cortex, and in fish the cerebellum is one of structures which support conditioning. Furthermore, Beritashvili and his associates found that short-term image memory evolved in fish, where it was measured in seconds; in reptiles, where it was measured in minutes; and in mammals, where it was measured in hours. Long-term image-driven memory appeared first in birds and lasted for months in baboons after single presentation of the object to be remembered. It may last for more than a month even in dogs (Beritashvili, 1971). All these data supported the hypothesis that animals' spatial goal-directed behavior is mediated by image-driven memory.

Through his peculiar approach, Beritashvili made an important contribution to the science of animal behavior (Tsagareli, 2007; 2015, Tsagareli & Doty, 2009) which bore a strong resemblance to the concepts of purposive behavior and "cognitive maps" developed concomitantly by Edward C. Tolman. Beritashvili's ideas concerning image-driven behavior anticipate modern ideas on animal behavior and mental representation (Allen, 2014). Unfortunately, because of the almost 30 years of the "iron curtain", Beritashvili was unable to communicate with Tolman and discuss the problems of animal behavior.

Tolman and His Concept of "Latent Learning"

Latent learning is a form of learning that occurs without any obvious reinforcement of the behavior or associations that are learned. It is not readily apparent to the researcher because it is not shown behaviorally until the animal is sufficiently motivated. In human subjects learning can occur by watching others and then modeling what they do or say. This is known as observational learning. There are specific steps in the process of modeling that must be followed if learning is to be successful. These steps include attention, retention, reproduction, and motivation. For example, children learn many things, both good and bad, simply by watching their parents, siblings, and others.

At the beginning of the 20th century, Edward L. Thorndike (1874-1949), who considered the ability to learn as the main indicator of intelligence and observing the solution of problems in the conditions of the experiment, concluded that the intelligence of animals allows them to act only by trial and error, and to learn the correct reaction gradually. His monograph, *Animal Intelligence* was the first systematic experimental study of the higher mental functions of animals under controlled laboratory conditions (Thorndike, 1911).

However, Edward Tolman (Figure 3) during the 1930s-1940s maintained that much more was going on inside the learning organism than mere responses to stimuli. In fact, Tolman proposed two main modifications to the prevailing view, stated in the first half of the 20th century that what went on inside the organism between these two the Stimulus-Response (S-R) events was neither observable nor measurable and, therefore, not subject to scientific investigation and, therefore, not important. So, according to this view, when a rat learned to run through a maze faster and with fewer errors, the learning process consisted of a succession of stimuli to which a succession of correct responses led to the reward of food at the end of the maze. This limited S-R connectionist view of behavior formed the core of behaviorism and dominated the first 50 years or so of psychology's short history (Hock, 2015).

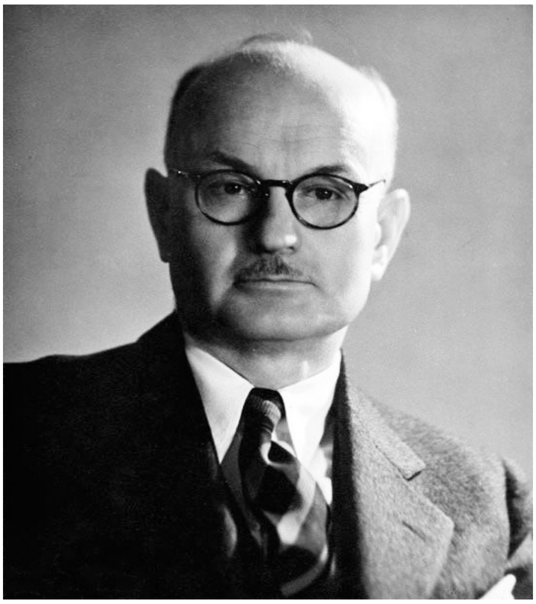

Figure 3. Edward C. Tolman (1886-1959), Prof. of University of California at Berkley (1918-1954), is best-known in cognitive behaviorism, for his concepts on latent learning, cognitive maps, and an intervening variable. E. C. Tolman was 46th President of the American Psychological Association in 1947-1948, and again in 1952-1953.

In this regard, Tolman's first modification was that the true nature and complexity of learning could not be fully understood without an examination of the internal mental processes that accompany the observable stimuli and responses (Hock, 2015). He stated:

> We believe that in the course of learning something like a field map of the environment gets established in the rat's brain. We agree with the other (stimulus-response) school that the rat running a maze is exposed to stimuli and is finally led as a result of these stimuli to the responses which actually occur. We feel, however, that the intervening brain processes are more complicated, more patterned, and often … more autonomous than do the stimulus-response psychologists. (Tolman, 1948, p. 192)

Although Tolman was firmly behaviorist in his methodology, he was not a radical behaviorist like Burrhus F. Skinner (1904-1990) using operant conditioning. Tolman worked on the phenomenon of "latent learning", a term first coined by Hugh C. Blodgett (1897-1950). Tolman performed the first experiment by making use of the paradigm of learning without reinforcement and used the term of latent learning (Blodgett, 1929).

The latent learning experiments of Tolman showed that rats learned the layout of complex mazes. After trials in which the rats were first rewarded in the goal box, they showed nearly error-free behavior on the next trial. From latent learning experiments Tolman concluded that learning is different from performance and occurs even when there is no clear evidence for it. Furthermore, the experiments showed that subjects acquire organized knowledge of the maze before learning about rewards. This conclusion, in particular, was inconsistent with the dominant behavioristic view that rewards determine which behaviors are learned (Seel, 2011).

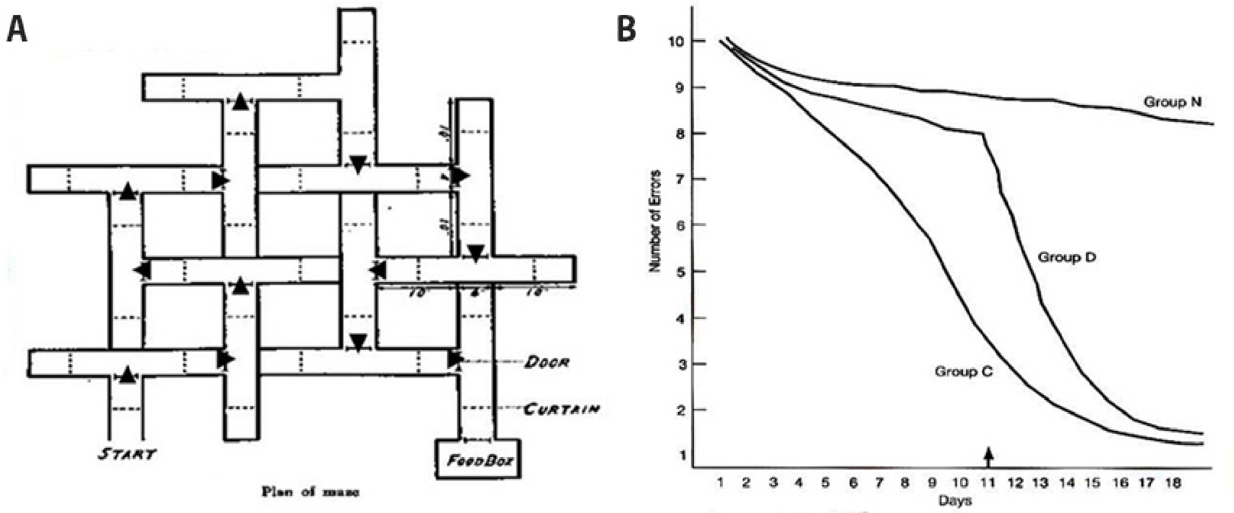

Figure 4. (A) Tolman and Honzik built a maze to investigate latent learning in rats. This study showed that rats actively process information rather than operating on a stimulus response relationship. (B) The learning curves show that three groups of rats had to find their way around a complex maze. At the end of the maze there was a food box. Some groups of rats got to eat the food, some did not. The delayed reward group (Group D, food after Day 11) learned the route on Days 1 to 10 and took longer to reach the end of the maze because there was no motivation for them to perform. From Day 11 onwards they had a motivation to perform (i.e. food) and reached the end before the reward group. These results show that between stimulus (the maze) and response (reaching the end of the maze) a mediational process was occurring the rats were actively processing information in their brains by mentally using their cognitive map. Notes. Group C: Control group (each day food); Group N: No reward (food); Group D: Delayed group (food on the 11th day) (adapted from Tolman & Honzik, 1930).

It was from investigations that Tolman and Honzik (1930) developed. Three groups of rats were required for typical latent-learning experiments in a maze (Figure 4A). The first group receives no food reward over the whole of experimental period of 18 days (Group N). The second group is given food each day (Group C). The third group is given food on the 11th day of the experiment (Group D) (Figure 4B). The errors in running the maze remain quite high for the first group of rats receiving no food reward. The second group of rats regularly rewarded the number of errors reduced from day to day as might be expected from normal learning procedures. However, the third group of rats showed a pattern of learning equivalent to the first group rats over the first 10 days. However, on the 11th day of the experiment, the day on which rats were first rewarded, they suddenly began to make as few errors as the second group (Figure 4B).

From these experiments, Tolman concluded that rats in the third group were learning the way about the maze in the first 10 days in spite of not being rewarded. These later-rewarded rats performed better at maze running than the regularly rewarded ones, suggesting that the later-rewarded rats thoroughly explored every aspect of the maze in the early trials and were therefore better equipped to run the maze in the final stages of the experiment (Tolman & Honzik, 1930).

Tolman's second study was called the "spatial orientation" experiment (Tolman, Ritchie, & Kalish, 1946). The S-R theorists had maintained that a rat knows where the food reward is only by running the maze (and experiencing all the S-R connections) to get to it. Tolman's spatial orientation technique was designed to show, rather, that rats trained in a maze know the location in space of the food reward relative to their starting position, even if the elements of the maze are radically changed or even removed (Hock, 2015).

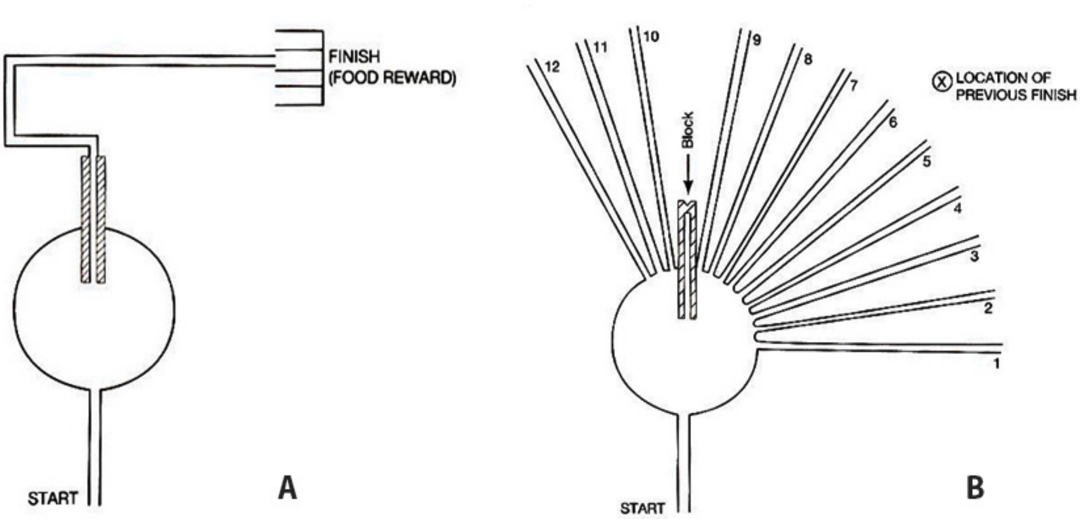

Figure 5. (A) Spatial orientation experiment with a simple maze. (B) Spatial orientation experiment with a sunburst maze, where rats have a choice of 12 possible alternative paths to get the food box (adapted from Tolman, 1948).

First, rats learned to run the simple maze shown in Figure 5A. Rats entered the maze at the start, and run across a round table and into the path leading, in a somewhat circuitous route, to a food reward at the end. This maze was a relatively simple and no problem for the rats that learned it to near perfection in 12 trials. Then the maze was changed to a sunburst pattern (Figure 5B).

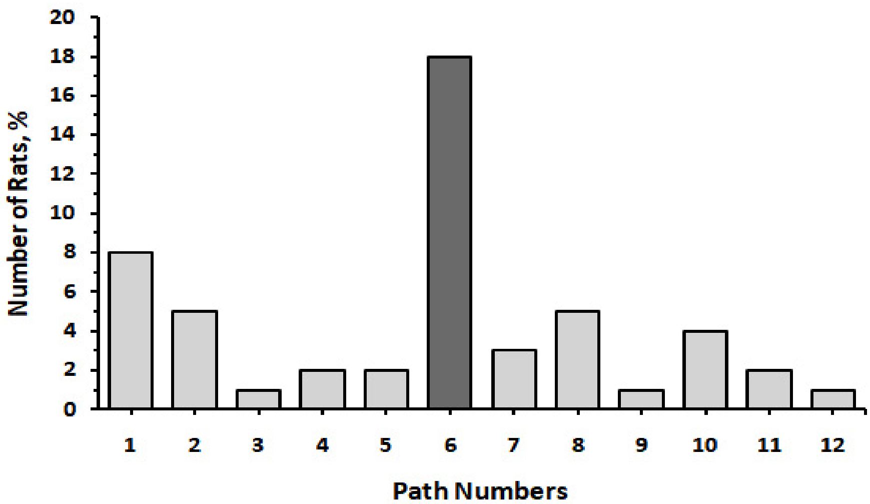

Figure 6. The result curves of spatial orientation experiment showing the number of rats choosing each path. Significantly more rats choose the path No. 6 than any other possible routes as it is the similar orientation as the simple maze. These results seem to indicate that the rats had learned not only to run rapidly down the original roundabout route but select one pointing rather directly towards the point where the food had been (adapted from Tolman, 1948).

When the trained rats tried to run their usual route, they found it blocked and had to return to the round table. There they had a choice of 12 possible alternate paths to try to get to where the food had been in the previous maze. The Figure 6 shows the number of rats choosing each of the 12 possible paths. The path No. 6, which ran to about four inches from where the food reward box had been placed in the previous maze, was chosen by significantly more rats than any other possible route. The rats had seemingly acquired not merely a strip map to the effect that the original specifically trained-on path led to food, but, rather, a wider, comprehensive map to the effect that food was located in a particular direction in the room. Here, Tolman was expanding his theory beyond the notion that rats, and potentially other organisms including humans, produce cognitive maps of the route from Point A to Point Z. He was demonstrating that the maps that are produced are not mere "strip maps" represented as A to B to C, and so on, to Z, but are much broader, comprehensive, or conceptual charts that give organisms a cognitive map of surrounding space (Hock, 2015).

Later, Tolman distinguished the five types of learning that are still under investigation: (1) approach learning, (2) escape learning, (3) avoidance learning, (4) choice-point learning, and (5) latent learning. All these forms of learning depend upon means-end readiness, i.e., goal-directed behavior, mediated by expectations, perceptions, representations, and other internal and external variables (Tolman, 1949).

Tolman's Purposive Behavior

Tolman introduced "purposive behaviorism" in the early 1920s and, although he continued to refine concepts, such as "latent learning" or "cognitive maps", over the next three decades, the essential features of his theory remained the same. He was introduced to behaviorism, as promoted by John B. Watson (1874-1949). However, Tolman did not accept Watsonian behaviorism wholeheartedly. Initially, in Tolman's purposive behaviorism, behavior implied a performance, the achievement of an altered relationship between the organism and its environment; behavior was functional and pragmatic; behavior involved motivation and cognition; and behavior revealed purpose. But for Tolman, in contrast to theorists such as William McDougall (1871-1938), who also advanced a purposive behaviorism, purpose was not a mentalistic concept (Innis, 1999).

In 1932, the ideas developed in a number of *Psychological Review* articles were presented as a system of psychology in the book *Purposive Behavior in Animals and Men*, which has continued to be the primary source for Tolman's ideas (Tolman, 1932). As a behaviorist, he developed a theory that encouraged expansion of the Watsonian scheme of behaviorism, and more so than did either Edwin R. Guthrie (1886-1959) or Clark L. Hull (1884-1952). Like Watson, Guthrie advocated a psychology of observable behavior consisting of muscular movement and glandular responses elicited by environmental stimuli. His theory of associations was in the tradition of Thorndike, asserting single principle to account for learning. Guthrie did not accept Thorndike's reinforcement principle based on the "low effect", but rather viewed Thorndike's secondary notion of associative shifting as the basis of learning (Guthrie's Contiguity Theory) (Brenan & Houde, 2017).

The core of Hull's analysis concerns the notion of intervening variables, described as unobservable entities employed by psychologists to account for observable behavior. Thus, from a purely behavioral perspective, Hull extended Watson's conceptualization of behavior in terms of peripheral Stimulus-Response (S-R) events to a consideration of central, organismic factors, called "intervening variables", described as Stimulus-Organism-Response (S-O-R) (Brenan & Houde, 2017).

As stated above, in his major work *Purposive Behavior* (1932), Tolman proposed a consideration of behavior that was molar, as opposed to molecular. He viewed "molar behavior" as a unified and complete act, which provides the proper unit for psychology. Underlying molecular elements, whether neural, muscular, or glandular, processes were not sufficient to account for the molar act. In this sense, Tolman departed from Watsonian behaviorism by opening psychology to the study of higher cognitive processes. His approach to molar behavior was nonreductive. In adhering to the molar level, Tolman argued that reductionism results in the loss of the purely psychological level, and explanations based upon molecular components are not adequate. Thus, for Tolman molar behavior is more than the sum of molecular elements (Brenan & Houde, 2017).

Tolman's Concept of "Cognitive Map"

In 1947, Edward Tolman delivered the 34th Annual Faculty Research Lecture at the University of California. The occasion, celebrating his long and distinguished career in the Psychology Department at Berkeley, provided Tolman with an opportunity to summarize the research that he and his disciples had carried out over more than three decades, and to differentiate his own system that he now called a field theory of learning, from the generally more popular S-R approach. The title of Tolman's talk, "Cognitive Maps in Rats and Men", reflected the key elements of his psychology at that relatively late stage of his career: a spatial metaphor for memory representation with the rat as a prototypical research subject and humans as the proper subject of his concern. Tolman concluded his faculty lecture by incorporating some of the ideas on the dynamics of human behavior into the cognitive map model then explicitly central to his general learning theory (Innis, 1999). His lecture was published one year later in *Psychological Review* in 1948 (Tolman, 1948).

Among other experiments, Tolman reviewed findings from a series of spatial orientation studies. These experiments, now still frequently cited in the literature, showed that the rats learned, albeit very generally, the location of important stimuli in their environment rather than learning merely a series of responses. For example, rats were trained on an elevated maze to take a long path to food and then, on a test trial, were presented a choice among many possible paths. The largest proportion of animals took the path that provided the shortest route to the food box, rather than the original path on which they were trained. This and similar studies provided strong support for the idea that the animals had a general representation of the situation, i.e., they had constructed a cognitive map (Innis, 1999).

Tolman's view of psychology relied heavily on many of the premises of the Gestalt psychologists. Indeed, he used the term Gestalt to describe holistic, insightful learning experiences. Moreover, his conception of behavior as a molar and his adoption of mental isomorphism were directly borrowed from Gestalt psychology. He used the latter construct to describe the central product of learning in terms of acquisition of field maps that exist in the brain as cognitive representation of the learned environment (Brenan & Houde, 2017).

Tolman's theoretical orientation was not as systematic in its approach as that of Hull. Tolman's criticism of the reduction of psychological events to the mechanical elements of S-R caused many Hullian researchers to pause and modify their views. Tolman's law of acquisition essentially focused on practice that builds up sign gestalts, or expectances. In maze learning experiments with rats, he described the acquisition of place learning, inferring acquisition of relationships or cognitive maps in the subject. Similarly, he demonstrated the expectancy of reinforcement in rats trained to one kind of reward and then switched to a more appealing food. Finally, he showed that latent learning occurs in rats, indicating that the quality of reinforcement can exert a differential effect on performance levels. In all of these experiments Tolman used cognitive explanations as "intervening variables" to show that behavior in organisms is governed by central, mediating process that goes beyond environmental input only (Brenan & Houde, 2017).

Tolman was often criticized for his lack of specific explanations of central mediation of cognitive learning as was Beritashvili for his image-driven memory. However, Tolman brought to behaviorism a new perspective that departed from the sterile reductionism of Watsonian behaviorism. Moreover, his repeated demonstration of performance "versus" learning differences showed that learning is not reducible to mere Stimulus-Response-Reinforcement elements, and Tolman gave a comprehensive explanation of cognitive learning prevalent in cognitive psychology.

Tolman proposed a rich theoretical structure in which "purpose" and "cognition" were central theoretical posits and potentially measurable intervening variables. For him, actions were infused with meaning; behavior was goal-directed that is, motivated and purposive (Innis, 1999). In the decades since Tolman's early studies, a great deal of research has supported his theories of cognitive learning. Perhaps the most notable outgrowth of Tolman's ideas and reasoning is the fact that today, one of the most active and influential subfields of the behavioral sciences is "cognitive psychology". This branch of psychology is in the business of studying internal, unobservable cognitive processes. Now it is generally accepted that the way a stimulus is processed mentally through perceiving, attending, thinking, expecting, remembering, and analyzing is at least as important in determining a behavioral response as the stimulus itself (Hock, 2015).

Edward C. Tolman's theories and studies of learning and cognition made a new contribution to spatial behavior. During the years when psychology was consumed with strict stimulus response learning theories that dismissed "unobservable" internal mental activity, Tolman was doing experiments demonstrating that complex internal cognitive activity occurred in rats' brain and that these mental processes could be studied without the necessity of observing them directly. Rats have an image in their "mind" of where the travel route to the reward box is located. This picture of "mental representation", he called a "cognitive map". Due to the significance of his work, Tolman is considered to be the founder of a direction about learning that is today called "cognitive-behaviorism" (Hock, 2015).

Beritashvili and Tolman: Two Destinies, One Discovery

The destinies of Beritashvili and Tolman are similar in some ways. Studying animal behavior by different experimental methods, they came to the same discovery, "image-driven" behavior by Beritashvili or a "cognitive map" by Tolman, both having a strong spatial component of navigation allowing animals (dogs or rats, respectively) to find the food in the shortest way and the shortest time. Tolman did not leave a systematic school of followers, as Beritashvili did. However, unlike Tolman, who passed away at the age of 73, Beritashvili worked actively until his last days and died in 1974, two weeks before turning 90. Unfortunately, Beritashvili's associates made no effort to record brain electrical waves in freely moving animals (cats or rats), similarly to John O'Keefe's contemporaneous work on rats.

It should be noted that both scientists were moral and principled personalities. Both stood opposed to authorities in their own countries, Beritashvili as an "anti-Pavlovian" in the Soviet Union, Tolman during the time of McCarthyism in the USA.

An examination of the works of Beritashvili and Tolman reveals that neither references the other. It is not unlikely that each was simply unaware of the other, perhaps because of the "iron curtain", and also because Tolman died before "Soviet Thaw" in the early 1960s.

It was a momentous event when the Nobel Prize in Physiology or Medicine 2014 was awarded to John O'Keefe for his discovery of "place cells" in the hippocampus, and to May-Britt Moser and Edvard I. Moser for their discoveries of "grid cells" in the entorhinal cortex, demonstrating a neuronal basis for the animal spatial navigation using a "cognitive map" of environment. And it is noteworthy that after more than half a century, the concepts of Tolman and Beritashvili were confirmed at the cellular level. However, it is rather disappointing that the name and contributions of Ivane Beritashvili went unacknowledged. For example, Beritashvili's name is not among the acknowledged forerunners in the scientific background document for that year's Nobel Prize in Physiology (Nadin, 2014). Beritashvili, as a pioneer of the study of spatial navigation in higher vertebrates, deserved mention in the Nobel background document alongside Tolman, who was acknowledged, and now Beritashvili's contributions warrant reappraisal.

In conclusion, Beritashvili's concept of image-driven behavior shares many elements with the modern concept of cognitive maps Tolman formulated and developed since the 1970s by neuroscientists in the West, including Howard Eichenbaum (1947-2017), who did much in this direction (Eichenbaum, 2014; Eichenbaum & Cohen, 2004), and Richard G. Morris, developing Morris water navigation task (1984). Beritashvili's contributions, along with Tolman's work, are the groundwork for modern studies of cognitive processes in animals and humans; recognition as such is not only warranted but is a step toward rectifying the apparent neglect of Beritashvili's scientific achievements and their place in the history of modern cognitive neuroscience.

Conflict of Interest

The author declares that the study was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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