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HOW THE BRAIN MAKES SENSE OF THE WORLD: MAY-BRITT MOSER AND THE 2014 NOBEL PRIZE IN PHYSIOLOGY OR MEDICINE

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I often get asked the question about
'how does it feel to be the first woman to…'
or, 'how does it feel to be a leading woman in science…'
but you know what? I don't think about myself as a woman
in these contexts, I think about myself as a human.
Thus, I feel like role model for all young people
who wants to do science – not only girls.

May-Britt Moser

For hundreds of years, thinkers have tried to unravel the mystery of the brain and the ways the brain makes sense of the world. In recent decades, prominent neuroscientists have come close to solving this phenomenon and have provided crucial information about the role of the brain in complex behavior. One of them is May-Britt Moser, a Norwegian psychologist and neuroscientist known for her work on spatial orientation and spatial memory specifically and cognition more generally and a co-recipient of the 2014 Nobel Prize in Physiology or Medicine. This paper aims to outline the main stages of her scientific activities.

K e y w o r d s: May-Britt Moser, 2014 Nobel Prize in Physiology or Medicine, neuroscience, hippocampus, spatial orientation, spatial learning, grid cells.

Are space and time emergent or fundamental, are they the maps or the territories? Thinkers have been debating these key issues since ancient times [1]. In the 18th century, the German philosopher Immanuel Kant argued that space was an a priori form of human intuition: "the presentation of space cannot be one that we take from the relations of outer appearance by means of experience; rather, only through the presentation of space is that outer experience possible in the first place", thus, "space is a necessary a priori presentation that underlies all outer intuitions" [2]. Although until almost the end of the 20th century neurophysiologists disagreed with the German thinker suggesting that animals' navigation in space was ensured by a sequence of their perception of sensory stimuli and the resulting motor responses, as often happens, the discoveries of modern science confirm the truths proclaimed by great thinker philosophers [3-5]. In 2014, the Nobel Prize in Physiology or Medicine was awarded to John O'Keefe, May-Britt Moser and Edvard I. Moser "for their discoveries of cells that constitute a positioning system in the brain" [6]. This remarkable contribution to science helped to confirm the Kant's hypothesis and interpret the innate system of orientation in space. Findings like these could hold the key to answering the important question of how the brain makes sense of the world.

One of the driving forces behind the research was the activity of May-Britt Moser who since childhood was imbued with the idea that "*even though you have nothing you can become something*" [7].

May-Britt Moser [8]

May-Britt Moser is a Norwegian psychologist and neuroscientist known for her work on spatial orientation and spatial memory specifically and cognition more generally [9]. She was born on January 4, 1963, in Fosnavåg, Norway. She grew up on a farm owned by her parents. While her father also worked as a carpenter, her mother took care of May-Britt and her four elder siblings. Her parents had to work hard, and this life experience taught the girl that "*work makes you happy*" [7] that later became the guiding star of her life path.

Being a very curious child, May-Britt Moser asked many questions about why animals behave like they do; she even studied the behaviour of snails as they ate grass. She thought about becoming a medical doctor or a veterinarian, but in her own words, she was "*too lazy to get better marks from high school so that I could attend medical school*" [10].

In 1982, May-Britt attended the University of Oslo, where she studied multiple subjects, including mathematics and physics. In Oslo May-Britt met Edvard Moser, her classmate in high school. It turned out that they had many common interests, and particularly the brain and how it works. Young people agreed on taking a clinical degree in psychology. In 1984, they became students of the same social psychology class, however, they decided not to pursue this career, but to take the path of studying the brain.

After doing behavioral research and learning a lot of behavioral theory along with experimental design in Terje Sagvolden's laboratory, May-Britt and Edvard were accepted in Per Andersen's laboratory. For psychologists being accepted into the neuroscience community was a challenge, but a passion to understand the brain and a willingness to work as long as it takes overcame all obstacles. To begin with, the young people were given a task to build a water maze lab from scratch that they successfully dealt with. The Andersen's idea was to study long-term potentiation in the living brain. To do this, tiny lesions of different sizes were made both in the dorsal and the ventral hippocampus of the rats. The study found that when the dorsal part of the hippocampus was damaged, the rats were unable to learn, while when the ventral part was damaged, they were fine and demonstrated good spatial orientation. Thus, it was clarified that it is the dorsal part of the hippocampus that is involved in spatial learning and memory [7]. The results of the research were presented to the public in a joint master's thesis and in the article published in "The Journal of Neuroscience" [11, 12].

It was not just their shared research that brought May-Britt and Edvard's lives together. Their relationship had changed from a friendship to a romance. They married in 1985 and had two daughters, Isabel Maria Moser in 1991 and Ailin Marlene Moser in 1995. May-Britt found a way to keep their children close by bringing them to the laboratory or to the conferences. She and her husband took turns taking care of the girls (Venta K. May-Britt Moser). Unlike many female researchers in other countries, May-Britt was not forced to choose between science and family. She states that she has never felt that her gender has been an impediment in her work: "*I see that female researchers in other countries have had a much tougher time than I have*", "*It's fantastic to live in a society where everyone is given an equal opportunity*" [13]. She firmly believes that gender differences should not limit or stop us from achieving our dreams, and both women and men benefit from working in the field where there is diversity, which brings new ideas, interesting challenges, and creativity [14, 15]. May-Britt's work was funded by the Research Council of Norway. Edvard Moser also became a PhD student.

May-Britt Moser investigated the correlations between the anatomical structure of the hippocampus and spatial learning in rats building a water maze literally from scratch. Using adult rats, Moser and her colleagues tested whether spatial training of rats can give changes in dendritic spine density in the CAl field of the hippocampus. It appeared that behavioral training induced structural change in the hippocampal cortex of adult rats [16]. The results of the research demonstrated that spatial learning in rats requires the dorsal but not the ventral hippocampus, which is essentially connected with subcortical areas; and efficient spatial learning required only 20-40% of the total hippocampus [17]. This work culminated in May-Britt Moser's doctoral thesis "Structural correlates of spatial learning in the hippocampus of adult rats" [18].

May-Britt Moser and Edvard Moser defended their PhDs in Oslo in 1995, while in Edinburgh with Richard Morris – the famous neuroscientist from the University of Edinburgh with whom they collaborated. May-Britt and Edvard also traveled to University College London, where they worked with a prominent neuroscientist and psychologist John O'Keefe. May-Britt Moser called this time "*one of the most learning-rich periods*" [7].

May-Britt and Edvard had hoped to stay at the O'Keefe's laboratory longer, they had also planned to go to the University of Arizona, but their plans changed dramatically after the opening up a position at the Norwegian University of Science and Technology in Trondheim. Though a couple was months away from defending their PhDs, not only did they successfully pass the interview, but they also got two positions.

The young couple of scientists not only taught, but also launched their own laboratory. And one of the first questions they were focused on was: how are the place cells (specialized neurons in the hippocampus, a brain region crucial for spatial navigation and memory) generated? What is the basis for them in the hippocampus? [7]. This research had a serious background, namely pioneering studies of spatial behavior in animals conducted by I. Beritashvili and E. Tolman.

The Georgian psychologist and one of the founders of the modern biobehavioral science Ivane Beritashvili [19, 20] demonstrated "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" [21]. The concept that animal behavior in the environment can be determined by a map-like representation of space was put forward by the American psychologist Edward Tolman in the 1940s. He believed that "in the course of learning something like a field map of the environment gets established in the rat's brain" [22]. E. Tolman distinguished between "narrow and strip-like maps" and "relatively broad and comprehensive maps" [22], pointing out that only the latter kinds of maps would support flexible behavior in a variable environment [23].

O'Keefe's research became the next step in the study of spatial behavior of the animals. J. O'Keefe and J. Dostrovsky discovered place cells in the early 1970s. Place cells are a subset of the excitatory pyramidal neurons in the hippocampus that fire at specific locations within an animal's local environment (place field) [24]. The researchers experimented with rats: the animals were placed in a special maze, and their brain activity was monitored using implanted electrodes. It turned out that some neurons in the rats' hippocampus reacted to the animal's location at a certain point in space. When the rats passed the route, a kind of cognitive map was formed in the brain. The research proved that the impulses of place cells do not simply reflect activity in sensory neurons but represent a complex mapping of space. Initially, the concept of the hippocampus involvement in spatial orientation was met with skepticism within the scientific community. However, after the discovery of place cells and multiply trials, the view on the problem changed. This discovery became the impetus for vigorous theoretical and experimental activity in studying the mechanism of functioning of place cells.

Upon receiving grants from the European Commission in 2000 and from the Research Council of Norway's Centre of Excellence programme, May-Britt Moser and Edvard Moser continued the investigation of the neural networks of the hippocampus and established the Centre for the Biology of Memory in 2002 [7]. In 1996, May-Britt Moser was appointed associate professor in biological psychology at the Department of Psychology at the Norwegian University of Science and Technology (NTNU) in Trondheim. She was promoted to a position as full professor of neuroscience at NTNU in 2000 [25].

Collaborating with prominent scientists from around the world, the Mosers conducted integrated neural network studies of hippocampal memory. With the assistance of Menno Witter (the Free University in Amsterdam), the Mosers were able to precisely place electrodes in the dorsocaudal medial entorhinal cortex (dMEC) of the rat brain that allowed them to record the activity of cells in response to specific behaviors. The cells in the dMEC appeared to be active in relation to an animals' position in the environment. However, unlike the activity of place cells, the activity of these cells occurred in a regular pattern: "as rats ran freely in their enclosures, spikes of activity at each electrode were not only evenly spaced but also similar in direction and size. The regular activity formed a grid of equilateral, tessellating triangles, as revealed by spatial analyses, which inspired the name grid cell" [26]. Grid cells were activated simultaneously in several places and formed nodes of an extended hexagonal lattice, which resembled the arrangement of holes in beehives. The largest cells of such a network were found in the ventral part of the cortex. In addition, scientists demonstrated that the formation of coordinate networks occurs not through the transformation (conversion) of sensory or motor signals, but due to complex network activity. It should be noted that the formation of a hexagonal neural network has not previously been observed in the functioning of any other brain areas [27].

Trying to unlock the mystery of the brain, the Mosers were eager to understand how grid cells operate and are generated and how they interact with other cell types and in more distant brain structures. In 2006, the Mosers found cells in the medial entorhinal cortex called head direction cells (neurons that fire when an animal's head points in a specific direction, regardless of their location, and are crucial for spatial navigation and maintaining a sense of direction) and in 2008, they found a third type of entorhinal cell type called border cells (neurons in the brain that respond to the presence of environmental boundaries, helping animals navigate and understand their surroundings) [28, 29]. They also found that grid cells, head direction cells, and border cells interacted with place cells in the hippocampus to determine orientation and navigation. The spatial representation system was described as an inner GPS, "the discovery of the brain's GPS system really represented a kind of a paradigm shift in how our brain – how specialized cells in the brain work together to create complicated thinking abilities. And that opened up whole new areas of understanding how our brains work in creating things like memory and planning" [30]. Thus, neuroscientists answered the question that philosophers had speculated about for eons and provided crucial information about the role of the brain in complex behavior.

In 2007, the Centre for the Biology of Memory was selected by the Kavli Foundation as the fourth Kavli neuroscience institute, an award that provides funding for basic research in perpetuity. In 2011, the Norwegian government funded the Norwegian Brain Initiative that allowed May-Britt Moser and Edvard Moser to open the Norwegian Brain Centre in 2012 as a collaboration between their laboratory and research groups working with medical imaging from St. Olavs Hospital. In 2012, the Mosers' laboratory was also awarded funding for a second 10-year-long Centre of Excellence by the Research Council of Norway [7]. Their new center was called the Centre for Neural Computation; and May-Britt Moser became the Founding Director of the Centre and remained in this position until 2022.

In 2022, Professor Moser and the research community at the Kavli Institute for Systems Neuroscience were awarded a new Centre of Excellence; and their new research centre is called the Centre for Algorithms in the Cortex that aims to reveal the algorithms that the cerebral cortex uses for cognitive functions. May-Britt Moser heads this Centre

May-Britt Moser in the laboratory, 2017 [31]

May-Britt Moser after receiving her Nobel Prize at the Stockholm Concert Hall [34]

[32, 33]. She is also the Founding Co-Director of the Kavli Institute for Systems Neuroscience.

The scientific community highly recognizes the activity of the Mosers. In 2014, the brain researchers received the most prestigious scientific award. The 2014 Nobel Prize in Physiology or Medicine was divided: one half awarded to John O'Keefe, the other half jointly to May-Britt Moser and Edvard I. Moser.

The discoveries of O'Keefe and the Mosers are undoubtedly among the most significant in neuroscience in recent decades. Their research has uncovered a completely new type of neuronal function, in which cells form a multi-component network that enables complex cognitive processes. Their work has both theoretical and practical significance and plays an important role in clinical practice, since some diseases of the nervous system, such as Alzheimer's disease, are accompanied by a disturbance of spatial orientation and spatial memory. May-Britt Moser emphasized that "*the entorhinal cortex and the hippocampus are relevant for many neurodegenerative diseases. For example, these brain areas are the first ones to show cell death in Alzheimer's disease (AD). And, interestingly, the first symptoms are problems with spatial navigation ability and memory*" [10]. Therefore, the Mosers' investigation could shed light on the mechanisms that lead to cell death in Alzheimer's disease. The neuroscientists have established the interdisciplinary Jebsen Centre for Alzheimer's Disease aiming to bring their research from the lab to patients [10, 35]. The study of complex neural structures is also very important for the rapidly developing field of neurocomputers and robotics [36-38].

In addition to the Nobel Prize, May-Britt Moser has received many honorary scientific awards and prizes, including 47th Louisa Gross Horwitz Prize for Biology or Biochemistry (Columbia University) (2013); 'Best female leader' award from Trondheim Business Society (Madame Beyer Award) (2013); 59th Karl Spencer Lashley Award (American Philosophical Society) (2014); etc.

May-Britt Moser's enormous success in the scientific field is largely determined by her broad worldview and active civic stance. Although May-Britt Moser and Edvard Moser divorced in 2016, they continue to work together. "*We have a common vision and it is stronger than most*", May-Britt Moser said [31]. This common vision manifests itself in scientific and social activities, community spirit, and high ethical standards. In times of full-scale war in Ukraine, May-Britt Moser and Edvard Moser help our country by signing a letter of Nobel laureates who support Ukraine and condemn the russian invasion, giving free online lectures to Ukrainian students, and joining the ambassador team for the fundraising platform UNITED24 [41].

Having a positive outlook, being energized and motivated to tackle challenges, May-Britt Moser feels happy: "*I have been lucky to live a fairy tale life, with a partner and a long-time collaborator, Edvard Ingjald Moser, who has supported me and helped me fulfil my dreams ever since we met. We have two wonderful daughters, Isabel Maria Moser and Ailin Marlene Moser. They are wise and loving human beings. Being an internationally recognised scientist brings a lot of adventures and a large network of friends and colleagues across the world. We have travelled to so many different places and learned so much*" [7].

The discoveries of O'Keefe and the Mosers explained how the brain lay out a map to let us understand where we are in space ("internal GPS") and demonstrated the cellular basis for higher cognitive functions. These insights set new tasks to be solved by a new generation of scientists.

ЯК МОЗОК ОСЯГАЄ СВІТ: МЕЙ-БРІТТ МОЗЕР І НОБЕЛІВСЬКА ПРЕМІЯ В ГАЛУЗІ ФІЗІОЛОГІЇ АБО МЕДИЦИНИ 2014 РОКУ

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Протягом століть мислителі намагалися розгадати таємницю мозку та зрозуміти те, як мозок усвідомлює світ. В останні десятиліття видатні нейробіологи наблизилися до розгадки цього феномену та надали важливу інформацію щодо ролі мозку в складній поведінці. Однією з них є Мей-Брітт Мозер, норвезький психолог і нейробіолог, яка відома своїми роботами з просторової орієнтації, просторової пам'яті та пізнання в цілому, а також є співодержувачем Нобелівської премії в галузі фізіології або медицини 2014 року. Ця стаття має на меті окреслити основні етапи її творчої діяльності.

Ключові слова: Мей-Брітт Мозер, Нобелівська премія в галузі фізіології або медицини 2014 року, нейронаука, гіпокамп, просторове орієнтування, просторове навчання.

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