ISSN: 2583-5386
DOI: doi.org/10.51219/JIH/oleg-v-gradov/80

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Journal of Integrated Health

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Vol: 5 & Iss: 1

Research Article

Vector Field Techniques for Detection of Neuronal Dynamics and Axonal Guidance / Axonal Pathfinding in the Presence of Mercury

Oleg V. Gradov*

Senior Researcher, Department of CHEMBIO, Russia

Citation: Gradov OV. Vector Field Techniques for Detection of Neuronal Dynamics and Axonal Guidance / Axonal Pathfinding in the Presence of Mercury. *J Integrated Health* 2026;5(1): 467-475. DOI: doi.org/10.51219/JIH/oleg-v-gradov/80

Received: 21 February, 2026; **Accepted:** 24 February, 2026; **Published:** 26 February, 2026

***Corresponding author:** Oleg V. Gradov, FRC CP RAS, Senior Researcher, Department of CHEMBIO, Russia, E-mail: o.v.gradov@gmail.com

ABSTRACT

The role of mercury in the development of various neuropathologies is well known. Biogeochemical cycles of mercury indicate the possibility of its introduction into various organisms (including humans) through the corresponding trophic chains. However, the literature analysis shows that until recent years there have been almost no works on the dynamic microscopic study (either in situ or in vivo) of the connectome involution in aquatic organisms (including fishes, marine mammals, etc.) under the mercury exposure. In this regard, we attempted to study the dynamics of morphogenesis and breakdown of the emerging connectome upon the mercury exposure. Dynamics of the axonal pathfinding / axonal guidance was carried out in a series of frames with an timecode (address-time code), on which it is possible to track the motion estimation vector fields of displacements and reaction-diffusion processes in the neural cell culture immediately after the introduction of a drop of either mercury or a mercury-containing liquid using capillary micropipettes. This paper describes the effects observed and discusses the possible mechanisms underlying them.

Keywords: Mercury, Ecotoxicology, Axonal guidance, Axonal pathfinding, Motion estimation, Vector fields

Introduction .1

The role of mercury in pathogenesis of various neuropathologies[1], including neurodegenerative diseases[2], is well known. In particular, it has been proven that mercury can cause the development of Alzheimer's disease[3-6]. It can also lead to brain tumors[7] and autism in children[8,9], caused by the disrupted machinery of neuro(morpho)genesis and disordered connectome development[10]. Such effects may be due to the mercury exposure at the early stages of development[11]. Similar effects are also observed in marine mammals[12] - inevitably exposed to mercury due to its presence in seawater[13-15].

Biogeochemical cycles of mercury in oceans and near coasts, in littoral zones, etc.[16-18] indicate the possibility of mercury incorporation into a wide variety of organisms through the relevant food chains - up to seafood-eating humans[19] and thus, actively (unlike most terrestrial organisms not engaged in the ocean "fishing"), carrying out mercury into the cycles of terrestrial organisms. In freshwater bodies (lakes[20,21], rivers and their sediments[22,23]) mercury can also exist and thus be distributed in freshwater and terrestrial biogeochemical cycles.

However, firstly, unlike the ocean, there is no a "single pool" of mercury in freshwater bodies with its transfer by the global currents or global migration of populations of individual species within the ocean; and secondly, high mercury concentrations in freshwater bodies in many cases are a secondary technogenic problem arising from the artificial mechanisms of the mercury extraction and transfer in the biosphere / techno sphere. In other words, the effect of mercury on neurogenesis of hydrobionts and, above all, oceanic fish and marine mammals is the most representative example of this effect and hence, can be used as a model.

However, until recent years, there are very scarce works on the effects of mercury on the development of the brain neural structure of marine mammals during natural or model exposure to mercury and, moreover, there are almost no works on dynamic observation of the development of their surviving brain slices upon such exposure by time-lapse microscopy and multi-angle 3D imaging techniques (confocal microscopy, SPIM, microtomography, holography and holographic microscopy), which would answer the question of Hg-inhibitor diffusion in space and time. How does axonal guiding / axonal pathfinding change with the introduction of the amounts of mercury characteristic of natural exposure into the nervous tissue? It is clear that in vivo exposure in marine mammals, most likely, does not reach the extreme effects similar to those observed from the long-term implanted amalgam carriers (such as the mercury-containing materials widely used in dentistry in the 20th century[24-29], which is associated with an increase in the Alzheimer's disease statistics observed by the end of the 20th century and beyond). However, at the level of single neurons or single contacts and groups of contacts of connectomes even a relatively low-intensity exposure should already have an effect but full-scale studies of this on marine mammals have not been conducted.

An even less explored issue is the reactivity of the fish nervous system to the introduction of mercury into the environment. Analyzing the current literature in recent years (since the author had not dealt with the fish nervous tissues since 2015[30], due to the lack of equipment and facilities required for their maintenance), we arrived to a paradoxical conclusion. Despite the increasing number of works postulating the toxic effect of mercury on fish (up to its toxicokinetics and biotransformation at various stages of this effect) and mercury contamination of fish under various hydrochemical conditions[19,31-40], the number of works describing and interpreting this effect at the cellular level, containing cytophysiological, immunohistochemical and morphometric data, allowing to quantify the effect with the topographic reference, is extremely small[41]. At the same time, it is obvious that direct extrapolation based on single studies is impossible for all fish, at least due to; the differences in neurogenesis and plasticity of the fish brain, depending on environmental conditions, up to the dependence on the climatic conditions[42,43]; the stress-dependence of morphogenesis and neuroanatomy of the fish brain up to neuroendocrinological / sexual determination44-50; social plasticity at different stages of development and under different living conditions[51-53]; taxonomic and microevolutionary differences between different fish classes in terms of neuronal organization and the prevalence of neurons of different ergicity, moreover, with the reference to the specific areas of brain, more or less reactive to mercury, depending on the morphophysiology or lifestyle of the particular fish species, which makes it impossible to compare such effects even in different fish taxa and not only to draw distant and unrepresentative parallels between the effects of mercury in fish and in mammals[54,55]. Moreover, due to topographic and anatomical reasons, differences in the effects of mercury on fish and marine mammals should also be reflected in the brain regeneration as well as in the effects of interhemispheric interaction and behavioral asymmetry[56,57].

Meanwhile, within the framework of the "Cellular Basis of Behavior" paradigm by the Nobel laureate E. Kandel, declared in his classic monograph of the same name[58], analysis of the hydrobiont behavior physiology should be based on cytoelectrophysiological and morphological analysis of their neurons, as well as the neural networks they form[58]. The study was carried out in gastropod mollusks of bearded seals from the family Aplysiidae (subclass Heterobranchia), as well as in the similar earlier works[59]. That is, pathological changes in the behavior of aquatic organisms, as well as in the behavior of the mammals eating them, caused by mercury, should affect the axonal guidance during the connectome formation and, consequently, the possibility of the signal propagation and transduction in the emerging neural network. All of the above is based on the neuronal morphogenesis, which is inhibited by mercury (which acts as an inhibitor of reaction-diffusion systems, but, as a rule, not as a classical inhibitor (sensu stricto) in the Turing model) and changes the directionality level / degree of the axonal pathfinding / axonal guidance, if such a heavy metal as mercury appears in the environment. Considering the regeneration capabilities of the fish neurons[60-62], which are evolutionarily different from those in amphibians and mammals, but still based on the same principles[63], we can say that not only the initial neurogenesis / neuromorphogenesis, but also neuroregeneration in fish, which also requires the use of axonal guidance mechanisms to restore the connectome, can be altered by the exposure to mercury on the mature fish brain.

After all of the above it seems that there should be a lot of works on the cultivation of the cells or nervous tissues and surviving brain slices of fish in mercury-enriched media, simulating the biological (marine) environment or biological fluids of the fish body contaminated with mercury. But, in fact, this is not true. A number of Eastern papers ask questions: what can we see in this kind of study, except from the calculation of the mortality statistics for the corresponding cells depending on the dose or exposure? Such a question formulation is fundamentally wrong. We should talk about the basic mechanisms underlying neuromorphogenesis and, in particular, axonal guidance and the mechanism should be studied at the level of the single cell response[58], which should be registered not on the fixed sections post factum, but during the cell development and regeneration (or degeneration of its processes / axons, if the effect is irreversible). To date, there are specific fluorescent probes for mercury ions[64], which makes it possible to establish colocalization between the content of mercury in a cell and biological degeneration of its structure or activity, determined by the intensity of "luminance" (fluorescence) of the other dyes (not interfering with the molecular probe for mercury in the spectral range). There are also methods of scanning electron microscopy in programmable atmospheres and in programmable liquid media with controlled ion concentrations, which make it

possible to trace local changes in the mercury concentrations using low-vacuum X-ray spectroscopy (either wavelength-dispersion or energy-dispersion detection) and map the sample composition by establishing colocalization of the mercury content at diffusion interfaces and the state / microstructure / ultrastructure of a biological sample in the given areas / ROI. Unfortunately, we are unaware of similar studies carried out on the neurons of marine mammals and even more on the fish neurons, although the experimental design seems to be rather obvious. Therefore, our approach described in this work is based on the simpler, but equally reliable methods providing dynamic study of the frames with the axonal pathfinding dynamics in a series of registrograms with a timecode, on which one can track the vector fields of movements and reaction-diffusion processes in the neural cell culture immediately after the introduction of a drop of mercury or a mercury-containing liquid using a capillary or a patch clamp pipette. In this paper we describe this method for the first time and test it on the data proving the effects of exposure to mercury on neurogenesis. We have also initiated works on more complex neural structures, but their results, due to the multiplicity of interacting elements of the brain neural structure, are more difficult to describe and interpret and require references to the unpublished data, that is why we decided to start publication from a simpler version of the experiment known since the end of the last century.

2. Materials and Methods

We used publicly available time-lapse footage of the axon growth and axonal guidance of the mollusk neurons in the presence of mercury (posted on the YouTube aggregator at:

https://youtu.be/XU8nSn5Ezd8;

https://youtu.be/FAWRYoYSAj4;

https://youtu.be/ewNvcFJEHbA;

https://youtu.be/Ipi3OneIw0A)

from the popular film “How Mercury Causes Brain Neuron Degeneration”, created by a team of authors from the University of Calgary (Faculty of Medicine, Dept. of Physiology and Biophysics). Sequences of frames taken before the introduction of mercury were taken as a control. To control the intrinsic dynamics of disturbances in vector fields during the mercury diffusion (under the conditions of advection and convection, which inevitably arise due to the temperature difference between the introduced substance and the cultivation medium), frames were taken for the first one and a half seconds after the toxicant introduction into the medium, until the currents were established, which made it possible to observe the dynamics and single neuron behavior without “convective artifacts”. As a control of the vector fields of the intrinsic neuron behavior, we used the frames taken after the stationary state establishment in the medium up to the final stage of involution (denudation) and destruction of trends in the connectome formation.

To analyze a series of film recordings / registrograms, we used the VirtualDub MSU Motion Estimation Filter developed by the Computer Graphics Laboratory at the Moscow State University (CS MSU Graphics & Media Lab; supervisor - Dmitry Vatolin; the authors of the algorithm - K. Simonyan and S. Grishin). Vector field visualization approach was used to analyze the object motions, which is also used in aero/hydrodynamics in PIV (particle image velocimetry)[65-68].

3. Results and Discussion

The results obtained and their description is shown in **(Figures 1-5)**. Briefly, the experiment demonstrates that:

- The structure of the vector fields of axonal guidance in the control (before the introduction of mercury into the liquid) demonstrates the presence of a high “search activity” of axons, spreading over the entire field of view - a kind of “probing the field”;
- After introducing a drop of Hg into the area free from cellular structures using a capillary or a patch clamp pipette, high-speed convective and advective flows are observed, indicating the beginning of mercury distribution in the medium;
- When mercury reaches the ends of the neuronal structures, denudation begins, accompanied by the contraction / degradation of the lateral filopodia, lamellipodia and protrusions, while the machinery of axonal path finding, the formation of connections (structural units of the connectome) is blocked and ceases to be active (since the vector fields of the corresponding structure dynamics are not registered any more);
- Further structural involution is indicated by the retrograde vector fields - there is a reduction in the growth cones of axons in all the neurons at an accessible distance, capable of participating in axonal path finding / axonal guidance;
- The terminal stage of the denudation processes is a stationary state, indicated by the absence of representative vector fields of motion estimation (however, at the initial period residual oscillations / fluctuations can be observed, resulting from the reversible short-wave contractions, which, apparently, are due to the automatism of the cell cytoskeleton elements and filopodia).

For convenience of the readers, description of the processes observed in the illustrations is given not in the text, but under the corresponding figures allowing to compare the development stages of the processes observed in a series of images. The author also tried not to overload this description with the terms from the field of molecular neurobiology in order to ensure the accessibility of the text and the method proposed for the readers working in chemical ecology. Based on the material presented, it can be concluded that the vector field method is effective in determining the axonal guidance dynamics in environments contaminated with mercury or mercury-containing toxicants. In addition, it is possible to speak about the specific cellular response mechanisms and stages of the effect of mercury exposure in laboratory conditions, using a staged interpretation of the flows visualized using vector fields. It can be noted that the elements of dynamics completely invisible to the human eye (fast-speed or too small-scale, as well as those carried out by the structures with sizes of the order of several pixels, which are usually noted as an obstacle to viewing the main picture) become visible in the vector field algorithm and, in the case of detection of their regular nature and connection with the object can generally be used to determine the intrinsic object’s properties. In this case all the questions about the cellular mechanisms of the mercury effect on hydrobiont neurons in natural conditions become solvable, since it is possible to reproduce almost any hydro

chemical medium of the arbitrary composition and to track even the most subtle cellular effects of axonal dynamics restructuring of in it either in real time or in post-processing.

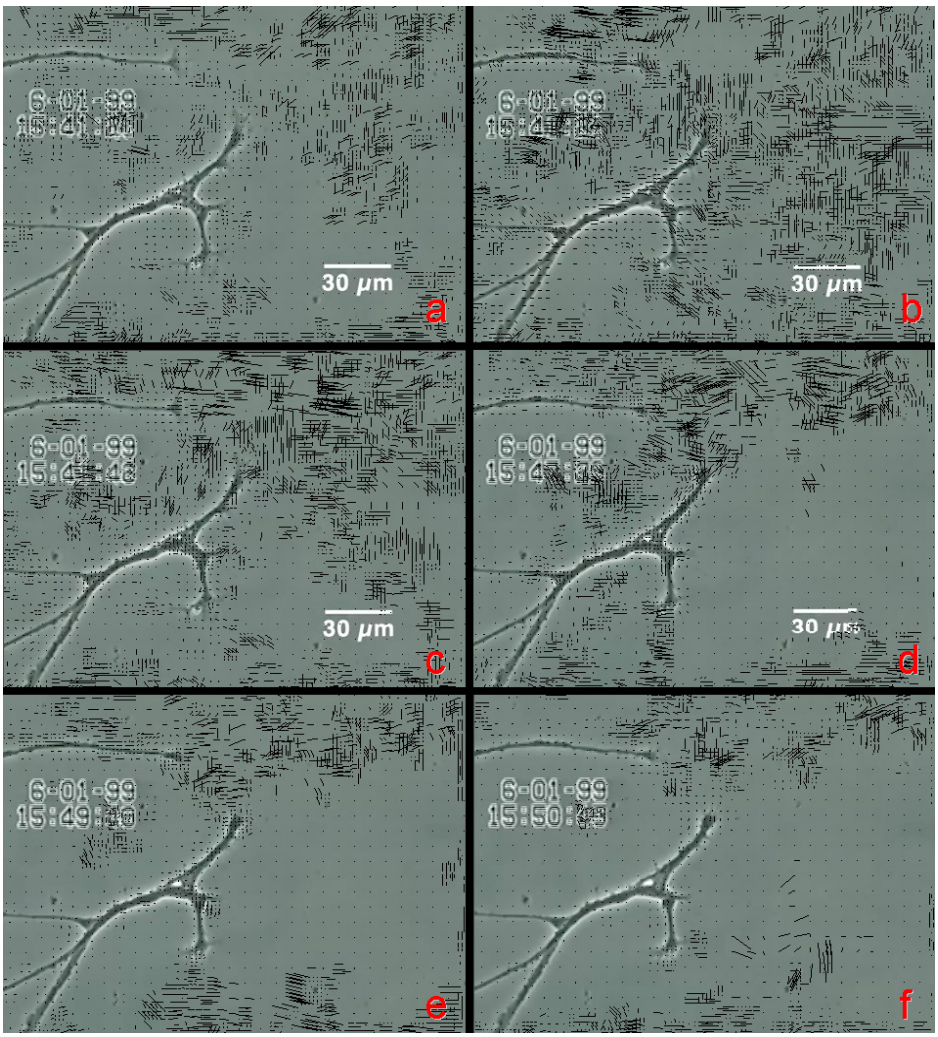

Figure 1: Normal neurodynamics during axonal pathfinding. It can be seen that both neurons generate directed impulses (co-directional "vector packets") in the axon region, which should lead to the connection formation. The branching neurofibers formed along these directions initially "probe" a wide area in search of the other neurons to create a connectome and then, having not received any response from the areas without neurons, focus their directions on the area where the response is expected to be from the axons of the neighboring neurons.

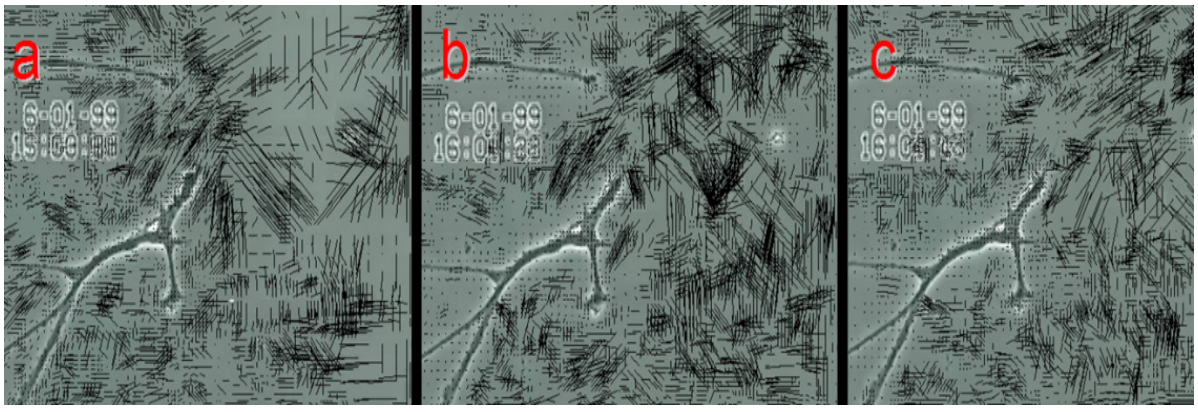

Figure 2: "High-speed" convective and advective flows in the medium after the introduction of Hg into the cell-free area using a capillary pipette or a patch clamp pipette.

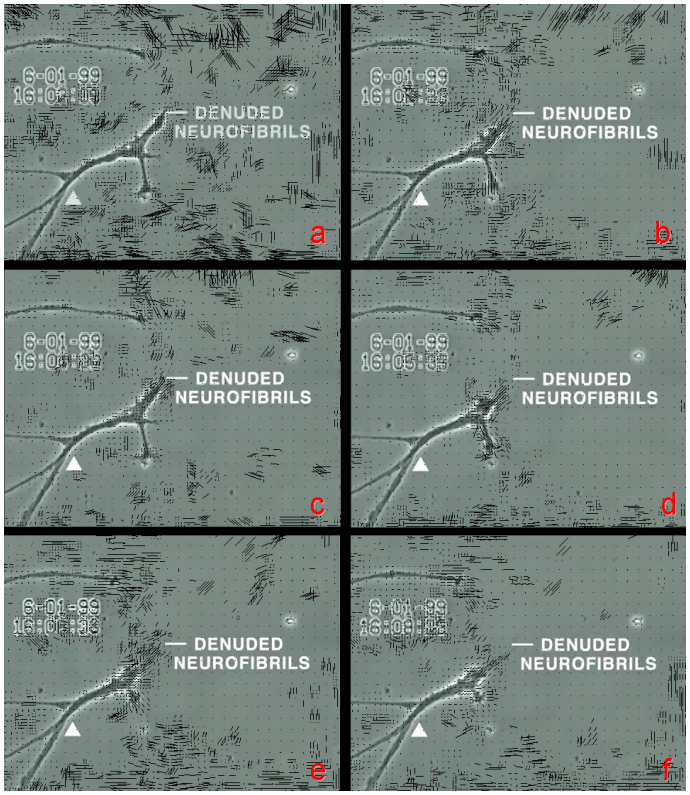

Figure 3: Beginning of denudation. One can observe the retrograde components of the fiber movements shown by the arrow. At the same time, the second fiber (above the timecode) inertially continues its axonal pathfinding until mercury diffusion reaches it. The vector fields directed from it towards the fiber undergoing denudation in order to establish connection with it are clearly observed **(Figure 3e-3f)**. However, compared to the control shown in **(Figure 1)**, the intensity of the axonal pathfinding from the second fiber is residual and the vector field propagation in the area of mercury diffusion has almost terminated (the first descriptor of neuro(morpho)genesis inhibition on the vector field maps is inhibition of the neuronal "pathfinding activity").

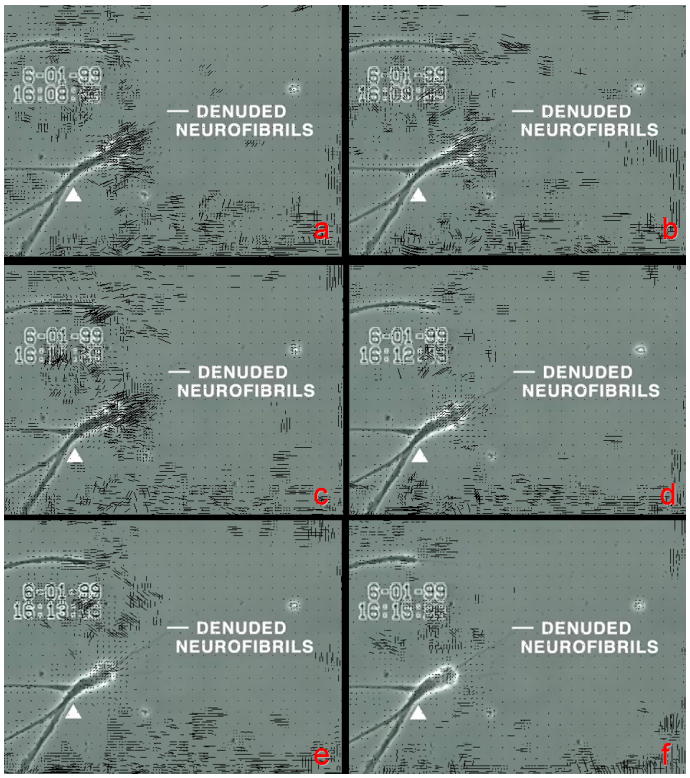

Figure 4: Development of the denudation processes. Further structural involution is detected by the intense retrograde paths visualized by the vortex phenomena on the vector field maps and high-speed (visible by the long vectors) stochastic retrograde motion **(Figure 4a-4c)**, lasting up to the establishment of a certain minimum stable somal form, which is further observed in the entire series of images **(Figure 4d-4f and Figure 5)**. Along with this, involution of the upper axon (located above the timecode) is observed, in which not only impulsive high-speed retrograde movements are fixed, synchronized with the similar phenomena in another participant of the axonal guidance process **(Figure 4c)**, but shortening also begins, similar to that observed in the first

neuron. At the same time, as the retrograde movements progress and the branching fibers shorten in both neurons, the "search field" (which in this sequence of frames and, in general, in this experiment, is equivalent to the mercury diffusion field) is cleared of the vector fields of mobility and axonal pathfinding.

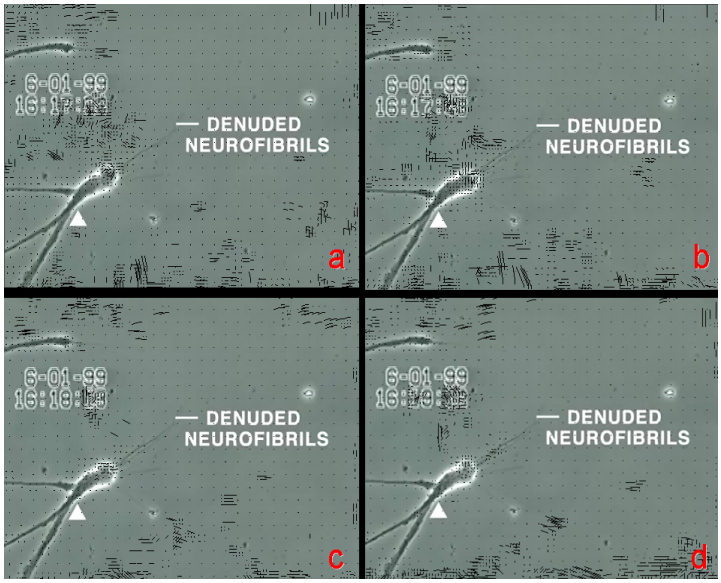

Figure 5: Terminal stage of the denudation process development (stationary state), characterized by the absence of representative vector fields of motion estimation (that is, from the point of view of mechanics, there is an almost complete lack of mobility). If in the first images of this series **(Figure 5a,5b)** one can still observe some movements in the medium within the area of the denuded neurofibrils, then in the last images **(Figure 5c,5d)** almost the entire field passes to a stationary state, excluding the terminal movement of the path elements that have not yet formed (automatism at the level of cytoskeletal elements, "supramolecular convulsions" in the jargon of colleagues from EMBL). At the same time, the second participant in the process, which has reached an almost stationary length, is still characterized (probably also due to the cytoskeleton automatism) by the tight retrograde (and reversible) movements at a fairly high speed, which can be registered by the "long" vector arrows in the upper part of the image in **(Figure 5c, 5d)**.

4. Conclusion

Production of the aqueous media simulating freshwater, oceanic or marine environments with an arbitrarily high complexity of the composition is not a significant technical problem at the moment, up to the models that include microbiological components, fluid models for specific geographical locations and specific light exposure levels imitating photo- and hydrochemistry of mercury and the presence of its specific dissolved or precipitated forms[32,69-76]. Moreover, in the presence of modern trend reconstructing models (which is a consequence of the "big data" analysis in natural ecosystems), adequate simulation is available not only for the known environmental conditions, but also for the arbitrary conditions for which a plausible calculation of the state in computational models is possible. That is, in fact, there are no obstacles to modeling not only statics and adaptation, but also the possible forms of the norm of reaction to the mercury content in the evolutionary process or in bio(geo/hydro-) chemical pathology.

Drawing parallels between the mercury bioavailability for consumers of different levels, including humans[77-81], it is possible to implement multilevel schemes of model systems, which will reproduce the conditions for mercury assimilation in ecological chains as a whole and not just in individual organisms. As a consequence, it is also possible to implement the schemes of installations with a modified environment (analogues of stop flow or continuous flow techniques, including their microfluidic implementations) to analyze the response of different neurons and for preparations of different types of aquatic organisms exposed to different hydrochemical conditions (in terms of Hg content). By applying to such "microchemostatic" systems vector-field methods for analyzing the results of microimaging obtained from inverted or lensless (which is suitable only for very large neurons) microscopes, it is possible to study the neuron pathfinding activity during axonal guidance depending on the environmental conditions and the contamination dynamics. In our opinion, such prospects can open a qualitatively new chapter in the history of mercury ecotoxicology, especially in terms of its neurophysiological and neuroembryological effects.

5. Acknowledgments

The author is grateful to M.A. Gradova for translation and proofreading of the text.

This paper is an extended version of the MBEGA-2022 conference paper[82], so the author expresses gratitude to the conference organizers for the opportunity to publish the primary material.

6. Conflict of Interests

The author has no conflict of interest to declare.

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