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POSSIBLE ROLE OF CENTRIOLES AS SENSOR CENTER IN CELLS

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ABSTRACT
In manuscript is proposed the hypothesis that the centrioles play role of sensor center in cells. The cilia and microtubules can regard as extracellular and intracellular sensor 'antennas' of centrioles by which they detect and controlled the cellular status.

Key words: centrioles, sensor, antennas, cilia, flagella.

INTRODUCTION

1. Centrosome, centriole, cilia and microtubules

The centrosome was discovered a century ago (1). The two major properties of the centrosome is its capacity to reproduce by duplication and its ability to nucleate microtubules.

Centrioles are the cylindrical structures found within the centrosomes of animal cells (a pair of centrioles forms the core of centrosome) and at the core of the mitotic spindle pole, which also act as basal bodies to nucleate formation of cilia and flagella. The replication and separation of centrioles during cell division is synchronous with the cell cycle. The absence of centrioles in the centrosome from other eukaryotic organisms has lead to the domination view that the centriole's pair is not relevant to centrosome activity. This view is also based on the fact that centrioles can be dispensable for spindle assembly, for example during the female meiosis some species (2). This arise the question, what then is the real function of centrioles, if they aren't needed for mitosis?

The other main function of the centrioles is to form the cilia and flagella. The cilia can exist in two main structural forms with different functions: motile cilia and non-motile (primary cilia). The primary cilium is a generally non-motile cilium that occurs singly on most cells in the vertebrate body. Recent findings reveal that the primary cilium is an antenna displaying specific receptors and relaying signals from these receptors to the cell body (3). Primary cilia contain a '9+0' axoneme, consisting of nine outer doublet microtubules but lacking the central pair of microtubules that is found in the '9+2' axoneme of most motile cilia (4). Microtubules control the beating of cilia and flagella, locomotor appendages of some cells, but they differ in their beating patterns. The spite of their ubiquity, the function of primary cilia is very poorly understood. Three major hypotheses for their function have been made. The first is that they are vestigial organelles inherits from an ancestor whose cells had motile cilia, and that they now have no purpose (5). A second hypothesis is that they are involved in controlling the cell cycle (6). Until recently, there has been no experimental evidence in support of these hypotheses. Recently, many observations have provided strong support for the hypothesis that primary cilia have a sensory function (3). Microtubules are the main constituents of the cellular cytoskeleton together with microtubule associated proteins, intermediary and actin filaments. Microtubules are dynamical instability structures because of it leads to reorganization of the cytoskeleton and therefore cellular morphology and

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functions. However, in highly differentiated cells like neurons there is a stable population of cytoskeletal microtubules. In most cells the majority of microtubules emanate from a microtubule-organizing center (centrioles) and radiates to the membrane and other structures of cells (7). Microtubules are rigid polymers that contribute the mechanical and elastic properties of cells. They resist various internal and external forces to maintain cell shape and they support motor proteins to generate the force required for cell movement and changes in shape.

2. Appearance of microtubules, centrioles and cilia in evolution

If we regard the sensor functions of Eukaryotic cells in evolution, we will observed that the appearance of microtubules, centrioles and cilia in cells is accompanied by increasing of metabolic and sensor activity of cells, and complexity of sensing functions **(Table 1).** Presence of centrioles correlates strictly with presence of cilia throughout eukaryotic phylogeny. The absence of cilia in higher land plants, fungi and red algae is accompanies by lack of centrioles or basal bodies. The presence of cilia in lower plants (moss, ferns), green algae, animals, ciliates, Euglena and Giardia is accompanies by presence of centrioles (8). It is observed that in all sensor mechanisms in which the cells act as photo-, chemo-, mechano- receptors (including neurons and neuronal processed) always participates microtubules, centrioles and cilia (9). In **Table 1** are given some cell types (with and without microtubules, centrioles and cilia) and their sensor ability.

Table 1. *Type of cells, presence of microtubules, centrioles, cilia and sensing functions*

CELL TYPE (references)	**NUCLEUS**	**CENTRIOLES**	**SENSING FUNCTION**	**TYPE OF FUNCTION**
Erythrocytes (Mammals) [10]	No	No	No	No
Erythrocytes (Poikilotherms, Aves) [10]	Yes (no-functioning)	marginal band of microtubules (MB) (circus-positioned)	No	No
Platelets [11]	No	1 centriole + MB Radial microtubules	Yes	Aggregation
Leukocytes [12]	Yes	2 centrioles Radial microtubules	Yes	Chemotaxis
Oocytes	Yes (no-functioning)	No	No	No
Spermatozoa	Yes (no-functioning)	2 centrioles	Yes	Chemotaxis
Higher plant cells [9a]	Yes	No	No	No
Yeast [13]	Yes	Radial positioned microtubules	Yes	Chemotaxis
Naegleria amebae [14]	No-Yes	0 – 2 centrioles	No-Yes	Chemotaxis
Fibroblast [15]	Yes	2 centrioles	Yes	Chemotaxis
Neurons [18]	Yes	2-12 centrioles	Yes	Neuronal
Photoreceptor cells [18]	Yes	2 centrioles	Yes	Photoreception
Mechanoreceptor cells [19, 20]	Yes	2 centrioles	Yes	Mechanorecep-tion
Chemoreceptor cells [19 , 20]	Yes	2 centrioles	Yes	Chemoreception

Example for the obvious role of centrioles in sensing mechanisms of cells give amoeba *Naegleria* (14). Under stress conditions (low temperature and food restriction) the growing amoebas disrupt growth, produce *de novo* two centrioles and are transformed in flagellates with chemotaxis ability. The **Table 1** gives the evidence that the presence of microtubules, centrioles and cilia in Eukaryotes always is accompanies with presence of any sensor functions of the cells.

HYPOTHESIS

The function of the centrioles could be summarized as follows:

Firstly, the centrioles are the main cell organelle which organized the synthesis, appearance and orientation of microtubules, sensor and motile flagellum.

Secondly, the centrioles are the first organelles which can accept the mechanical (tension) and others sensor signals from microtubules, sensor cilia (9+0) and flagellum (9+2). Consequently, the cell necessary to have centrioles is mutually connected to cell necessary to receive information from extracellular and intracellular cell 'antennas' –microtubules and cilia.

Giving in the mind these facts we arises the hypothesis that the centrioles play role simultaneously- as motile and sensor center in cells. The cilia and microtubules can regard as extracellular and intracellular sensor 'antennas' of centrioles. The centrioles received the sensor signals from cilia and microtubule and produce the 'effector' reactions of cell level. Accordingly this hypothesis in the cells could have two main informational centers: NUCLEUS center (genes or DNA library) which functioned like cell 'informational center' and CENTRIOLES center (sensor center) for detection of external and internal sensor signals-**Figure 1**.

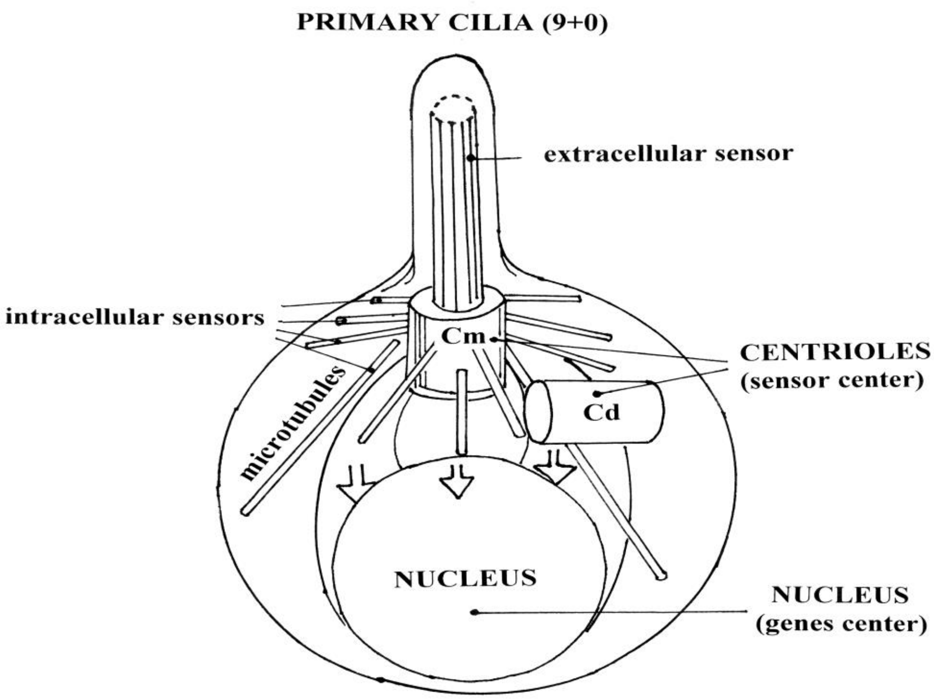

Figure 1. A scheme of living cell with nucleus (genes center) and centrioles (sensor center).

Between centrioles and nucleus always exists structural and functional connection-**Figure 2**.The nucleus and centrioles are places nearly in the cytoplasm and often are connected by 'nucleus-basal body connector'. Activity of the nucleus and centrioles changes recurrently and concurrently. During G1, G2 and S phase the nucleus activity dominated, while during M and G0 phases of cell cycle the centioles activity dominated.

Accordingly the hypothesis:

1. The microtubules act as 'intracellular sensor antennas'. Cilia act as 'extracellular sensor antennas'.
2. Intracellular microtubules and extracellular cilia send signals to centrioles as acceptors of signals.
3. Under influence of sensor signals the centrioles initiated effector's reactions of the cell.

To work as sensor center the centrioles need to satisfied two main conditions:

1. Only complex of mother and daughter centrioles can work as sensor center.
2. The daughter centriole must be synthesized from the mother centriole.

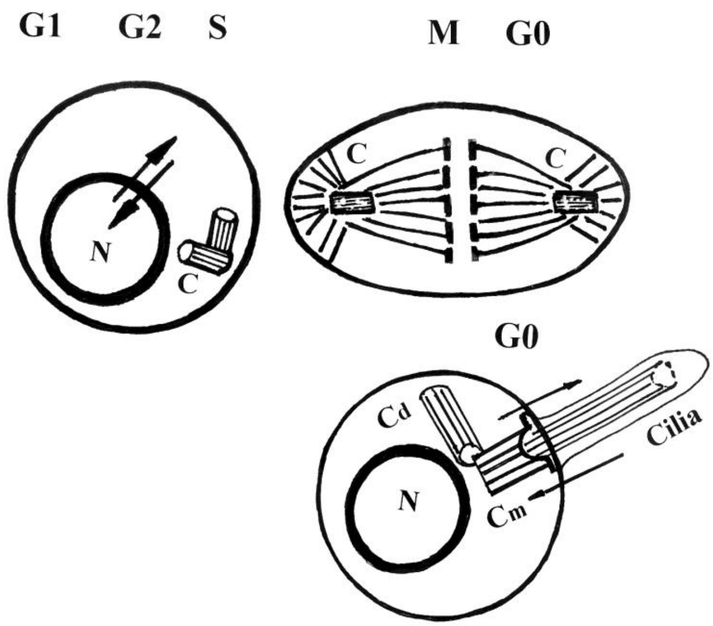

Figure 2. *The nucleus (N) and centrioles (C) activity during G1, G2, S, M and G0 phases of the cell cycle. During G1, G2 and S phases the current information occurs predominantly between nucleus and cytoplasm of the cells. During M and G0 phases the current information occurs prediminantly between the centrioles and the external area of the cells.*

Indeed the primary cilium is extended from a basal body that is analogous to the pre-existing mature centriole in the cells. By contrast, in multi-ciliated epithelia, ciliogenesis begins with centriole multiplication that yields up to several hundred basal bodies.

SOME EXPERIMENTAL EVIDENCES SUPPORTING THE HYPOTHESIS

Microtubules sensation. The microtubules can sense some extracellular chemical attractants (in Yeast) that leads to polarization of cells and oriented growth of cells to extracellular chemo-attractant stimuli (13). Microtubules can locate some biochemical molecules (RNA) (15, 16), some cell structures like chromosomes (during cell mitosis) as well as the mitochondria during the full cell cycle Microtubules can act on activity of some enzymes too. Thus, the microtubules work as ‘intracellular sensor antenna’ similarly to primary and sensor cilia that work as ‘extracellular sensor antennas’.

Cilia sensation. Cilia can interpret environmental sensing many stimuli as nutrient, oxygen concentration, calcium level, kinetic flow (flow signaling, pressure, touch, vibration), morphogenetic, olfactory, hormonal (chemical). There are some data that sensory reception is an attribute of both primary cilia and motile cilia (20).

Centrioles effector functions under intracellular and extracellular sensor signaling. The centrioles can regulates cell functions using signals and information from microtubules and cilia. For example, the centrioles can regulate the cell proliferation, cell differentiation, cell transcription, cell migration, cell polarity, tissue morphology (17) and others. The centrioles, possibly can play role of epigenetic center too (16). The centrioles can made these functions trough reorganized cytoskeleton and position of cell organelles, to make moving of the cells, to send information to nucleus and cytoplasm, to switch genes programs and others.

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