

Cyclodextrins in Autophagy

The 2016 Nobel Prize in physiology and medicine will be awarded to Yoshinori Ohsumi for his discoveries of mechanism for autophagy.

The press release of Nobel Assembly at Karolinska Institutet [1] says "The word *autophagy* originates from the Greek words *auto-*, meaning 'self', and *phagein*, meaning 'to eat'. Thus, autophagy denotes 'self eating'. This concept emerged during the 1960's, when researchers first observed that the cell could destroy its own contents by enclosing it in membranes, forming sack-like vesicles that were transported to a recycling compartment, called the *lysosome*, for degradation. Difficulties in studying the phenomenon meant that little was known until, in a series of brilliant experiments in the early 1990's, Yoshinori Ohsumi used baker's yeast to identify genes essential for autophagy. He then went on to elucidate the underlying mechanisms for autophagy in yeast and showed that similar sophisticated machinery is used in our cells.

Ohsumi's discoveries led to a new paradigm in our understanding of how the cell recycles its content. His discoveries opened the path to understanding the fundamental importance of autophagy in many physiological processes, such as in the adaptation to starvation or response to infection. Mutations in autophagy genes can cause disease, and the autophagic process is involved in several conditions including cancer and neurological disease."

In this editorial the effect of cyclodextrins on autophagy is reviewed.

Autophagy is a mechanism to digest cells' own components and its importance in many physiological and pathological processes is being recognized. Autophagosomes are generated and fused with late endosomes to form amphisomes, which subsequently fuse with lysosomes forming autolysosomes. These large vacuoles (autolysosomes) digest damaged cell organelles and proteins *via* acidic lysosomal hydrolases [2]. This is a catabolic process resulting in degradation of abnormal protein aggregates, excess or damaged organelles. Products of the digestion are moved into the cytoplasm for further utilization or expelled by exocytosis. Autophagy is generally activated by shortage of nutrients for maintaining the energy homeostasis by recycling of cytosolic components. Compromised autophagy is associated with various pathological conditions, such as neurodegenerative diseases and infections.

Neurodegenerative diseases, such as Alzheimer's disease, Parkinson's disease, Huntington's disease, and amyotrophic lateral sclerosis, share a common cellular and molecular pathogenetic mechanism involving aberrant misfolded protein or peptide aggregation and deposition. Autophagy represents a major route for degradation of aggregated cellular proteins and dysfunctional organelles. Emerging studies have demonstrated that up-regulation of autophagy can lead to decreased levels of these toxic aggregate-prone proteins, and is beneficial in the context of aging and various models of neurodegenerative diseases [3].

Autophagy involves dynamic rearrangement of cellular membranes. Based on the effect of various CDs on the cellular membranes (removal of cholesterol by BCD derivatives, especially by methylated BCDs and removal of phospholipids by ACD and its methylated derivatives [4]) it seems obvious that CDs can influence autophagy and help also in understanding the effect of the membrane components such as cholesterol in this cellular process.

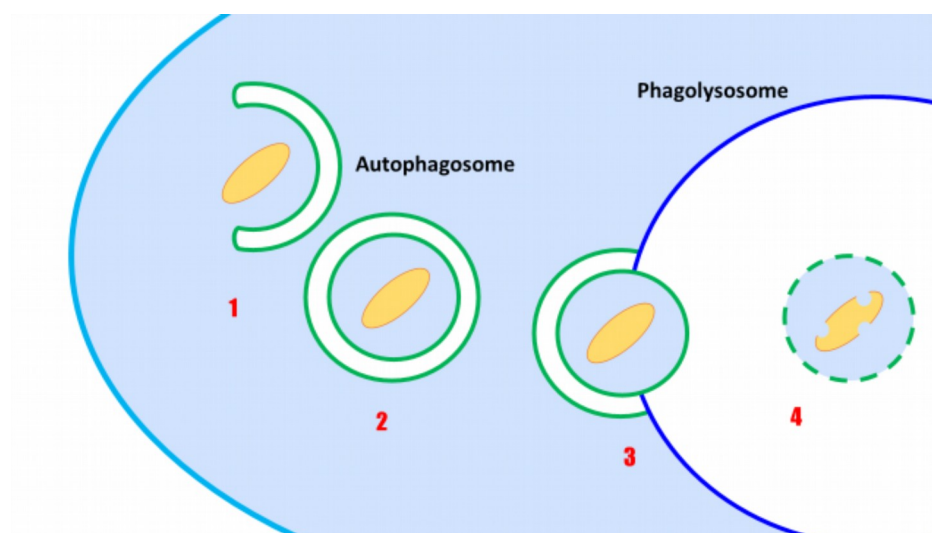


Figure 1. Scheme of autophagy.

Signal transduction induces autophagy (1) autophagosome, a double membrane vesicle (300 to 900 nm) is formed (2). The autophagosome docks with the cytosol and after fusion of the membranes (4) the breakdown within the autolysosome (or autophagolysosome) starts allowing recycling of the degraded autophagic body and its hydrolyzed cargo (amino acids, fatty acids, cholesterol, sugars, and nucleotides). (Redrawn after [5])

Inefficient autophagic activity has been linked to several neurodegenerative diseases characterized by aberrant accumulation of intracellular substrates. In these genetic lysosomal disorders HPBCD was found to reduce the symptoms most probably *via* activation of the impaired autophagy. In Niemann Pick type C (NPC) disease cholesterol accumulation can be reduced by HPBCD treatment [6], while in neuronal ceroid lipofuchsinoses (NCLs) the intracellular accumulation of autofluorescent ceroid lipopigments (proteolipids) is decreased [7]. Saposin C deficiency is a rare variant of Gaucher disease characterized by accumulation of glucosylceramide, ceramide, unesterified cholesterol and other lipids in the endo-lysosomal compartment that can be moderated by HPBCD [8].



CD Effect on the Formation of Vacuoles

Cholesterol depletion was claimed to induce autophagy [9]: after depletion of the cellular cholesterol in human fibroblasts using either 5 mM methyl-BCD or nystatin, or mevastatin and mevalonolactone, autophagic vacuoles indistinguishable from those seen after amino acid starvation were observed. It was suggested that a decrease in cholesterol activated autophagy with the mechanism involving phosphatidylinositol 3-kinase signaling.

In human NPC1 neurons and fibroblast cells lysosomal cholesterol accumulation leads to autophagy disruption, which in turn leads to mitochondrial fragmentation in NPC1. Mitochondrial fragmentation is an exceptionally severe phenotype in NPC1 neurons causing abnormal accumulation of mitochondrial proteins. Accumulation of mitochondria and other substrates that are ordinarily rapidly cleared by the autophagic pathway as well as mitochondrial fragmentation may cause defective energy production and generation of toxic oxygen species that can ultimately affect neuronal health and function. Mobilization of cholesterol from the lysosomal compartment increased the turnover of microtubule-associated protein-1 light chain-3 (LC3) protein, the most widely used marker of autophagosomes. Autophagy disruption and mitochondrial fragmentation was rescued by CD treatment by affecting early stages of autophagosome [10].

Yan et al. found that methyl-BCD induced not only apoptotic cell death but also autophagic cell death of K562 cell line (chronic myeloid leukemia cells)[11]. As a marker of autophagy the LC3 was used. The accumulation of LC3-positive structures was observed in cells treated with methyl-BCD compared with untreated cells. The cell death induced by methyl-BCD (1 mmol) was significantly attenuated when chloroquine, autophagy inhibitor (10 mmol) was added simultaneously. Rearrangement of the cell membrane (disruption of lipid rafts) by methyl-BCD resulted in downregulation of extracellular signal-regulated kinase/sphingosine kinase 1 (ERK/SPK1) signaling inducing cell death.

In another study, however, methyl BCD did not induce the formation of autophagic vacuoles in KB cells although it drastically inhibited the tumor growth after intratumoral injection to Colon-26 cells-bearing mice. In this study methyl BCD induced apoptosis in tumor cells not autophagy [12]. On the other hand, modifying methyl-BCD with folate groups for targeting to the tumor cells expressing folate receptors the obtained folate-appended methyl-BCD (FA-M-BCD) induced the formation of autophagic vacuoles in KB cells. The antitumor activity of FA-M-BCD, not methyl-BCD, was inhibited by the addition of chloroquine and bafilomycin A1, autophagy inhibitors [13].

On the contrary to these observations a combined therapy of HPBCD, allopregnanolone and miglustat resulted in decreased number of autophagosomes containing electron-dense myelin-like inclusions in Purkinje cells [14].



CD Effect on Fusion of Bilayers

The autophagic/lysosomal system includes a variety of vesicular compartments which undergo dynamic fusion events. Changes in membrane lipid composition, induced either *in vitro*, by treatment with 25 mM methyl-BCD, or *in vivo*, by subjecting animals to a high-fat-diet challenge (60% kcal in fat) reduced the fusion of phagosome containing ingested particles with lysosome containing hydrolytic enzymes. The reduction reached 70% of that observed in untreated fractions or from animals under a normal regular diet [15].

Compromised autophagy was seen in disease-affected organs of mice in NPC, which lack NPC1 protein (NPC1 mutant mice) [16]. This protein has a role in autophagy and its loss of function impairs autophagy-specific traffic. The fusion of autophagosomes and late endosomes to form amphisomes is impaired in NPC1 mutant cells. Inhibition of autophagy causes cholesterol accumulation, therefore the upregulation of autophagy, especially facilitating the autophagosome–lysosome fusion, seems to be a potential treatment strategy. HPBCD used as a cholesterol-depleting drug against NPC disease blocks autophagic flux at higher concentration. A dose and time-dependent elevation of autophagosomes concentration was observed showing that the maturation of autophagosomes was inhibited. Probably the fusion of membranes need a certain level of cholesterol and a high depletion of cholesterol impairs this process. Application of low doses of HPBCD still able to remove cholesterol but not significantly disturbing autophagy was suggested.

The more recent therapy implies a combination of low dose HPBCD and an autophagy stimulator (rapamycin or carbamazepine) [17, 18]. Stimulating autophagy partially restores the function of the pathway by facilitating autophagosome maturation and cargo degradation possibly through direct autophagosome–lysosome fusion independent of amphisome (autophagosome–endosome fusion) formation.

CD Effect on Expulsion of Autophagolysosomes

The accumulation of autophagolysosomes was observed in erythrocytes of mice in an unusual anemia with defective lipoprotein metabolism. This hinders the normal maturation and results in abnormal morphology. It was proved that phagolysosome expulsion was inhibited in the presence of markedly increased cellular cholesterol [19]. By incubating these erythrocytes *in vitro* with the cholesterol-sequestering agent methyl-BCD the expulsion was dramatically accelerated.

Meske *et al.* found that in neurons of NPC disease the clearance of autophagosomes was delayed, which lead to an accumulation of autophagic vacuoles within the lysosomal compartment [20]. Lowering the abnormal lipid load of the organelles with cyclodextrin was found to be sufficient to correct the autophagic flux and prevent premature death of NPC1 $-/-$ neurons under autophagic stress. Similarly in NCLs cells and Saposin C deficient fibroblasts (cells from other neurodegenerative diseases) the treatment with HPBCD results in



enhancement of the cellular autophagic clearance capacity. The mechanism in Saposin C deficiency might be the activation of the transcription factor EB, a master regulator of lysosomal function and autophagy. HPBCD administration promotes transcription factor EB-mediated clearance of proteolipid aggregates that accumulate due to inefficient activity of the lysosome-autophagy system in cells derived from a patient with a lysosomal storage disorder [6]. In Sap C cells the reduced levels and catalytic activities of proteases, cathepsin B and D lead to lysosome dysfunction and delayed degradation of autolysosomes and these processes are diminished by depletion of cholesterol and ceramide with HPBCD.

CDs effect in the antibacterial and antiviral defense mechanism

As a first step of defense against infection, phagocytes are alarmed and capture the invaders (bacteria or viruses) then engulf them (phagocytosis). Entry of pathogen bacteria and viruses into macrophages starts with the fusion of membranes of the invader and the host cell. This fusion requires the presence of cholesterol in the plasma membrane [21]. Cholesterol depletion with methyl-beta-cyclodextrin on pre-existing phagosomes in mouse bone marrow-derived macrophages infected with *Mycobacterium avium* resulted in a loosening of the close apposition between the phagosome membrane and the mycobacterial surface, but helped in fusion with lysosomes. The resulting phagolysosomes then autonomously executed autophagy. After 5 h of depletion, intact mycobacteria had accumulated in large auto-phagolysosomes. These observations indicate that, cholesterol depletion (i) resulted in phagosome maturation and fusion with lysosomes and (ii) caused mycobacterium-containing phagolysosomes to autonomously undergo autophagy. Furthermore, (iii) mycobacteria were not killed in auto-phagolysosomes, and (iv) cholesterol replenishment enabled mycobacterium to rescue itself from autophagic phagolysosomes to again reside individually in phagosomes which no longer fused with lysosomes [22].

The intracellular respiratory pathogen *Legionella pneumophila* or the extracellular uropathogen *Escherichia coli* enter macrophages by a cholesterol-sensitive mechanism. They immediately reside in vacuoles rich in glycosylphosphatidylinositol moieties and the autophagy enzyme Atg7. When macrophages were pretreated with methyl-beta-cyclodextrin or filipin, fewer Atg7-rich vacuoles were observed [23].

CD complexes as inducers of autophagy

Some complexes as inducers of autophagic cell deaths (in these works the effect of CD on autophagy has not been studied):

Benzaldehyde/BCD inclusion complex induces autophagic cell death in cancer cell lines [24]. Electron microscopy demonstrated that the destruction of mitochondrial structure and digestion of broken organelles by secondary lysosomes in all of these cells was induced.



A novel curcuminoid [4-(13,5-bis(2-chlorobenzylidene-4-oxo-piperidin-1-yl)-4-oxo-2-butenoic acid)] (CLEFMA) as a potent anti-proliferative agent, was found to induce autophagic cell death in lung cancer cells. CLEFMA encapsulated by HPBCD and formulated into liposomes retained the antiproliferative potency of free CLEFMA, while maintaining its non-toxic nature in normal lung fibroblasts [25].

The cyclic tetrameric derivative of Indole-3-carbinol (Ctet) formulated in GCD efficiently inhibited cellular proliferation in breast cancer cell lines. The cellular assays showed that the autophagic lysosomal activity was significantly up-regulated [26].

Summary

As cellular membranes play important role in autophagy, their modulation by CDs modifies this important house-keeping process of the cells. The results of various studies seem to be controversial partly because different cell types, different CDs were used at different concentrations.

The accumulation of the autophagosomes, the intermediary products of autophagy, was interpreted both as a sign of activated and impaired autophagy. HPBCD treatment at high concentration leads to cholesterol depletion in an extent which leads to hindered fusion of the cellular membranes and this way to the diminished fusion of autophagosomes with lysosomes or to reduced expulsion of the autophagolysosomes. At low HPBCD concentrations, however, the autophagy is not perturbed or might be even improved. Recently a combination of cholesterol removal by HPBCD and autophagy stimulation by rapamycin or carbamazepine seems to be a promising strategy in the treatment of impaired autophagy in lysosomal storage disorders, such as Niemann Pick type C. Further studies are needed to understand the effect of CDs on autophagy and especially to learn how these effects can be utilized in the therapy of various illnesses including neurodegenerative diseases.

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Éva Fenyvesi

CycloLab Cyclodextrin R&D Laboratory, Ltd.
Budapest, HUNGARY



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Homepage: www.cyclolab.hu

H-1525 P.O. 435, Budapest,
Hungary

Tel.: (+361)347-6060

Fax.: (+361)347-6068

e-mail: cyclolab@cyclolab.hu