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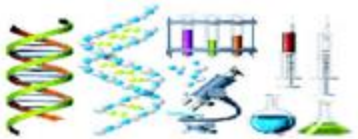

Study of mechanisms of protein aggregation and mechanisms of action of aggregation suppressors

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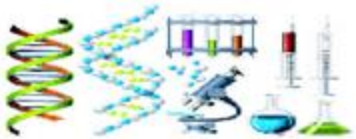

One of the important directions of modern biochemistry and molecular biology is investigation of the mechanisms of protein folding. Misfolding results in the formation of protein aggregates, which may exhibit cellular toxicity. The protective mechanisms of the cell that are realized with participation of molecular chaperones provide suppression of aggregation of non-native proteins. The main goal of the studies being conducted by the research team of Prof. B.I.Kurganov is the elaboration of the methodology for quantitative estimating anti-aggregation activity of protein and chemical chaperones. The methodology includes the original approaches which are developed by Kurganov and coworkers and allow estimating the adsorption capacity of the protein chaperones with respect to a target-protein and the affinity of the chemical chaperones with respect to a target-protein.

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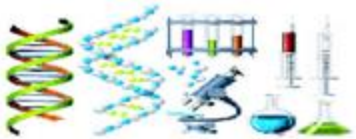

To study the action of agents possessing chaperone-like activity on the kinetics of aggregation of target-proteins, the new approaches elaborated by Kurganov and coworkers are applied. These approaches consist of the determination of the order of aggregation with respect to protein on the basis of analysis of the initial rates of aggregation measured at various concentrations of the protein, the determination of the size of the start aggregates, establishing the kinetic regime of aggregation on the basis of analysis of the dependences of the hydrodynamic radius of the protein aggregates on time, estimation of the adsorption capacity of protein chaperone with respect to target protein, estimation of the affinity of chemical chaperone with respect to target protein and estimation of the effects of synergism and antagonism for combined testing of chaperones.

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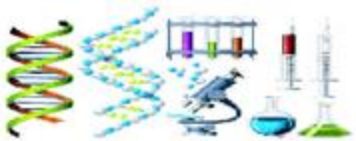

Researchers run into the problems of protein aggregation when performing biotechnological tasks (storage of protein preparations, refolding of recombinant proteins and so on) or developing medicinal drugs intended for the treatment of neurodegenerative and other diseases caused by accumulation of protein aggregates in the cell. Since chaperones of different classes possess ability of interacting with non-native proteins, the comparative investigation of mechanisms of protective action of different chaperones is a topic of great current interest. Formerly such studies were being conducted only on the qualitative level and elaboration of strict quantitative methods for estimation of chaperone-like activity is required to complete assigned task.

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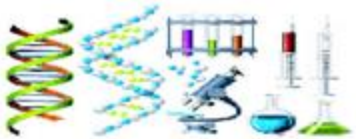

Main scientific achievements of the research team of Prof. B.I.Kurganov

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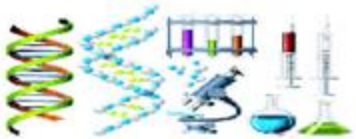

1. To establish the mechanism of aggregation of proteins containing disulphide bonds in the presence of a reducing agent (dithiothreitol), the kinetics of dithiothreitol-induced aggregation of alpha-lactalbumin and insulin was studied using dynamic light scattering. A new mechanism of amorphous aggregation of proteins has been experimentally substantiated (Bumagina Z.M., Gurvits B.Y., Artemova N.V., Muranov K.O., Kurganov B.I., Biophys. Chem., 2010, v. 146, p. 108-117; Bumagina Z., Gurvits B., Artemova N., Muranov K., Kurganov B., Int. J. Mol. Sci., 2010, v. 11, p. 4556-4579). The initial stage of aggregation is the formation of the start aggregates containing hundreds of denatured protein molecules. Further aggregation proceeds as a result of sticking of the start aggregates and aggregates of higher order in the regime of diffusion-limited regime where the sticking probability for the colliding particles is equal to unity.

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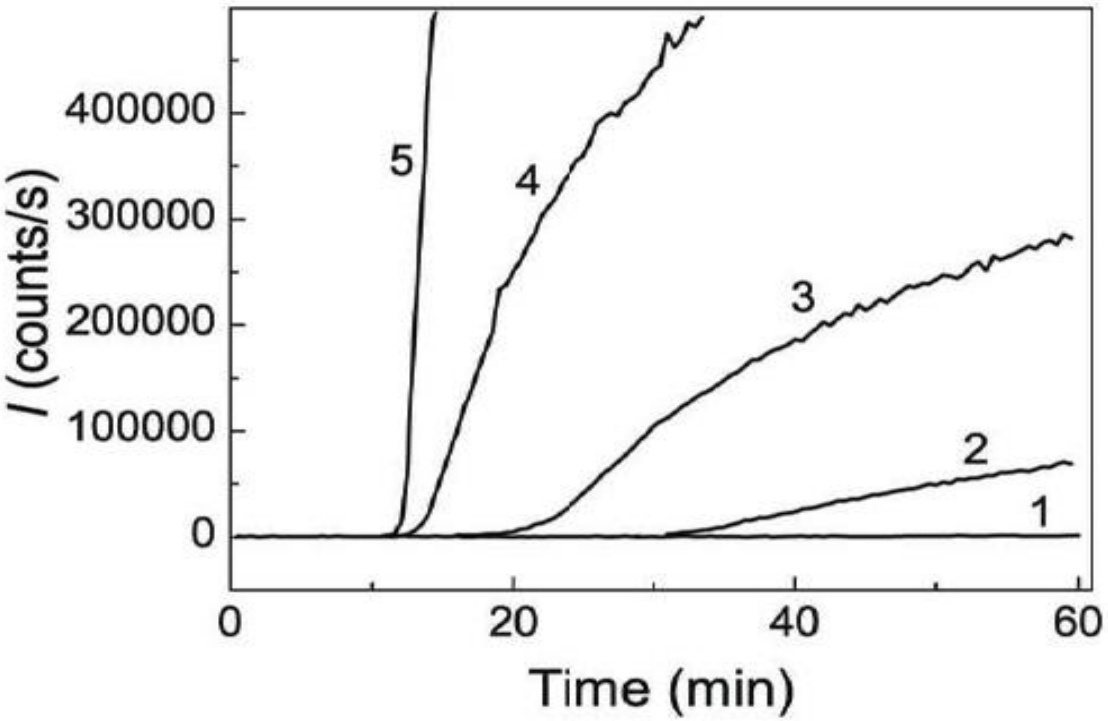
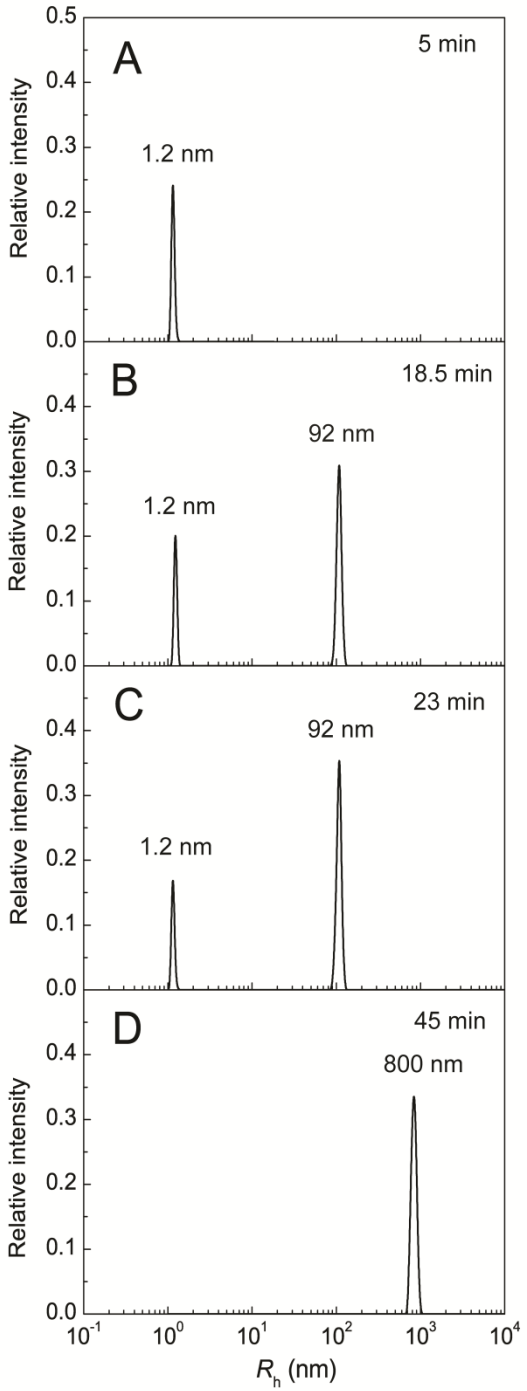


Kinetics of dithiothreitol-induced aggregation of α-lactalbumin at 37 °C in 50 mM sodium phosphate buffer, pH 6.8, containing 0.15 M NaCl and 1 mM EGTA.

The final concentration of DTT was 20 mM. The dependences of the light scattering intensity (*I*) on time. The concentrations of α-lactalbumin were as follows: 0.2 (1), 0.4 (2), 0.6 (3), 0.8 (4) and 1.6 (5) mg/mL.



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The distribution of the particles by size for α-lactalbumin (0.6 mg/mL) incubated at 37 °C in 50 mM sodium phosphate buffer, pH 6.8, containing 0.15 M NaCl, 1 mM EGTA and 20 mM DTT, for 6 (A), 18.5 (B), 23 (C) and 45 (D) min.

Peak with R_h = 1.2 nm corresponds to the non-aggregated from of α-lactalbumin. Peak with R_h = 92 nm corresponds to the start aggregates.

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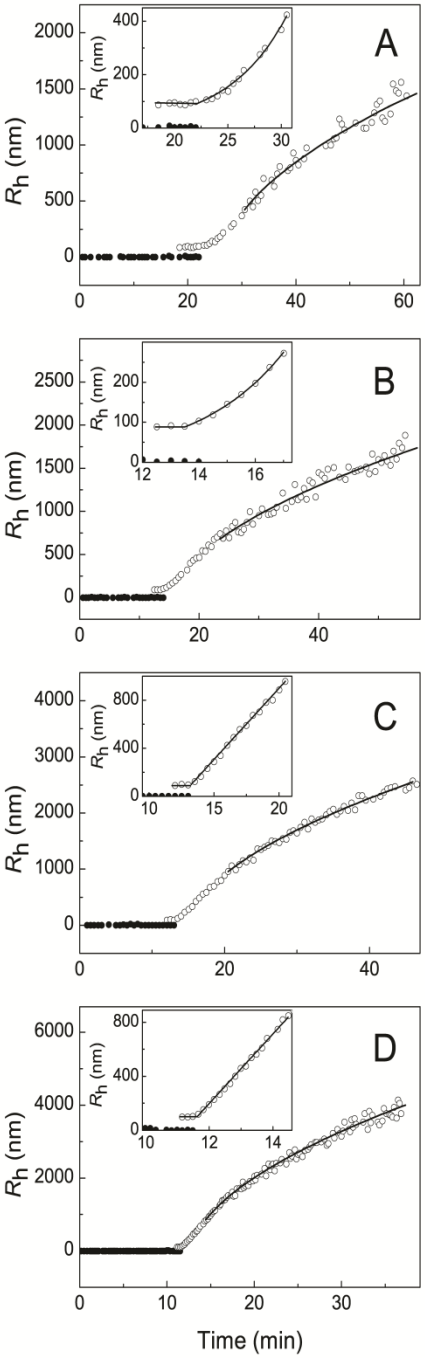

Analysis of the size of the particles in the solution of α-lactalbumin after the addition of DTT (the final concentration of DTT was 20 mM).

The dependences of the hydrodynamic radius (R_h) of the non-aggregated form of α-lactalbumin (solid circles) and protein aggregates (open circles) on time. The concentrations of α-lactalbumin were as follows: 0.6 (A), 0.8 (B), 1.0 (C) and 1.6 (D) mg mL^{-1}. Insets show the dependences of R_h on time with the expanded ordinate axis. The horizontal lines correspond to the hydrodynamic radius of start aggregates ($R_{h,0}$).

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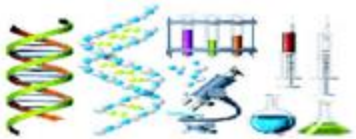

2. When testing the effect of cyclodextrins on protein aggregation, the acceleration of thermal aggregation of glyceraldehyde-3-phopshate dehydrogenase from rabbit skeletal muscles in the presence of 2-hydroxypropyl-beta-cyclodextrin was observed (Maloletkina O.I., Markosyan K.A., Asriyants R.A., Orlov V.N., Kurganov B.I., Dokl. Biochem. Biophys., 2009, v. 427, p. 199-201; Maloletkina O.I., Markossian K.A., Asryants R.A., Semenyuk P.I., Makeeva V.F., Kurganov B.I., Int. J. Biol. Macromol., 2010, v. 46, p. 487-492). This result is surprising since cyclodextrins, as a rule, have the capability to suppress protein aggregation. The paradoxical effect of 2-hydroxypropyl-beta-cyclodextrin was explained as a result of destabilization of the protein molecule induced by binding of 2-hydroxypropyl-beta-cyclodextrin to unfolding intermediates.

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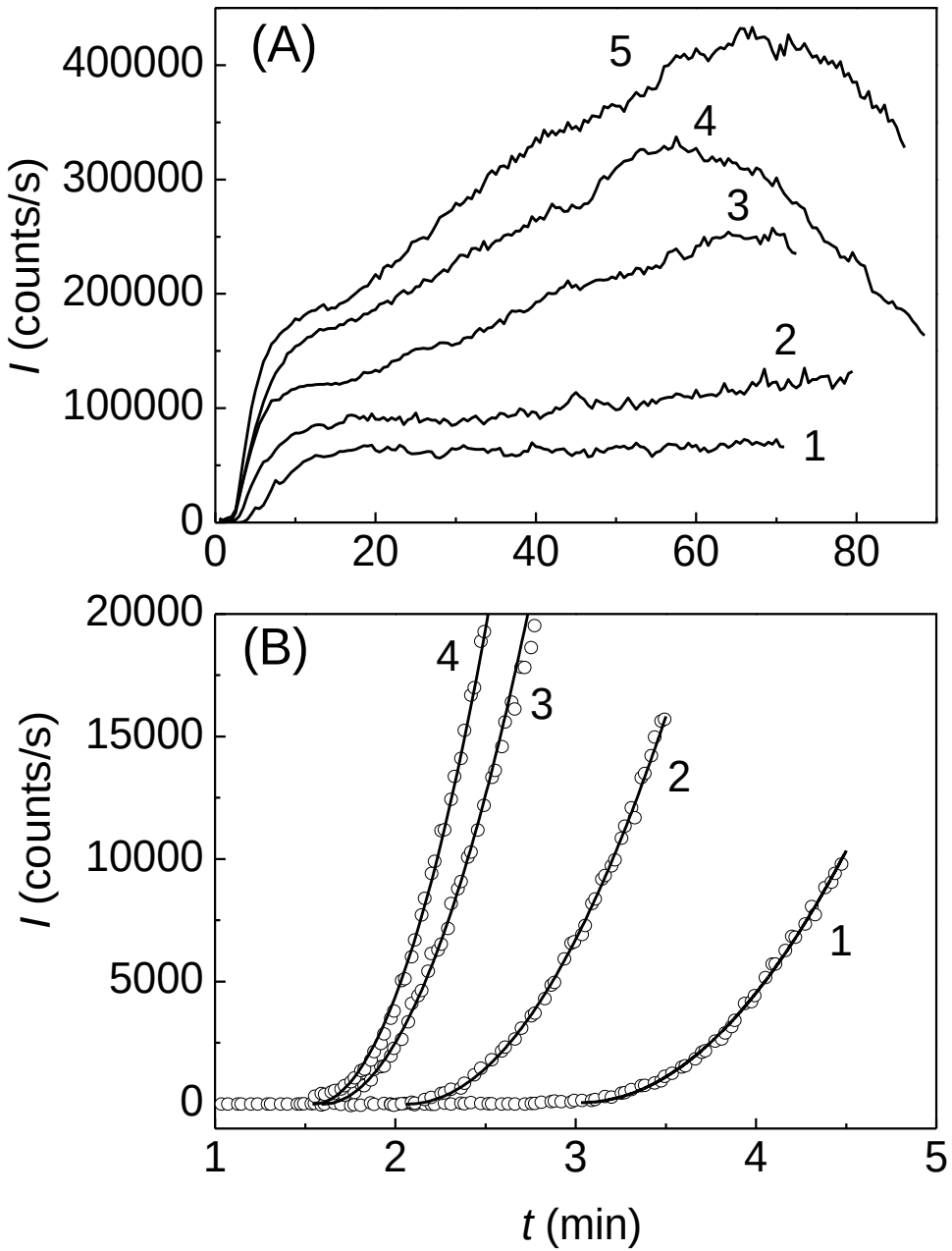

Effect of 2-hydroxypropyl-β-cyclodextrin (HP-β-CD) on thermal aggregation of glyceraldehyde-3-phopshate dehydrogenase from rabbit skeletal muscles (0.4 mg/mL; 2.8 μM) at 45 °C (10 mM Na-phosphate buffer, pH 7.5, 0.1 M NaCl).

(A) The dependences of the light scattering intensity (*I*) at 632.8 nm on time obtained in the absence of HP-β-CD (curve 1) and in the presence of 4, 31, 46 and 76 mM HP-β-CD (curves 2-5, respectively).

(B) Analysis of the initial parts of the dependences of the light scattering intensity on time. The concentrations of HP-β-CD were the following: (1) 0, (2) 4, (3) 31, and (4) 61 mM. The solid curves were calculated from the equation: $I = K_{agg}(t - t_0)^2$, where K_{agg} is a parameter characterizing the initial rate of aggregation and t_0 is the length of lag period.

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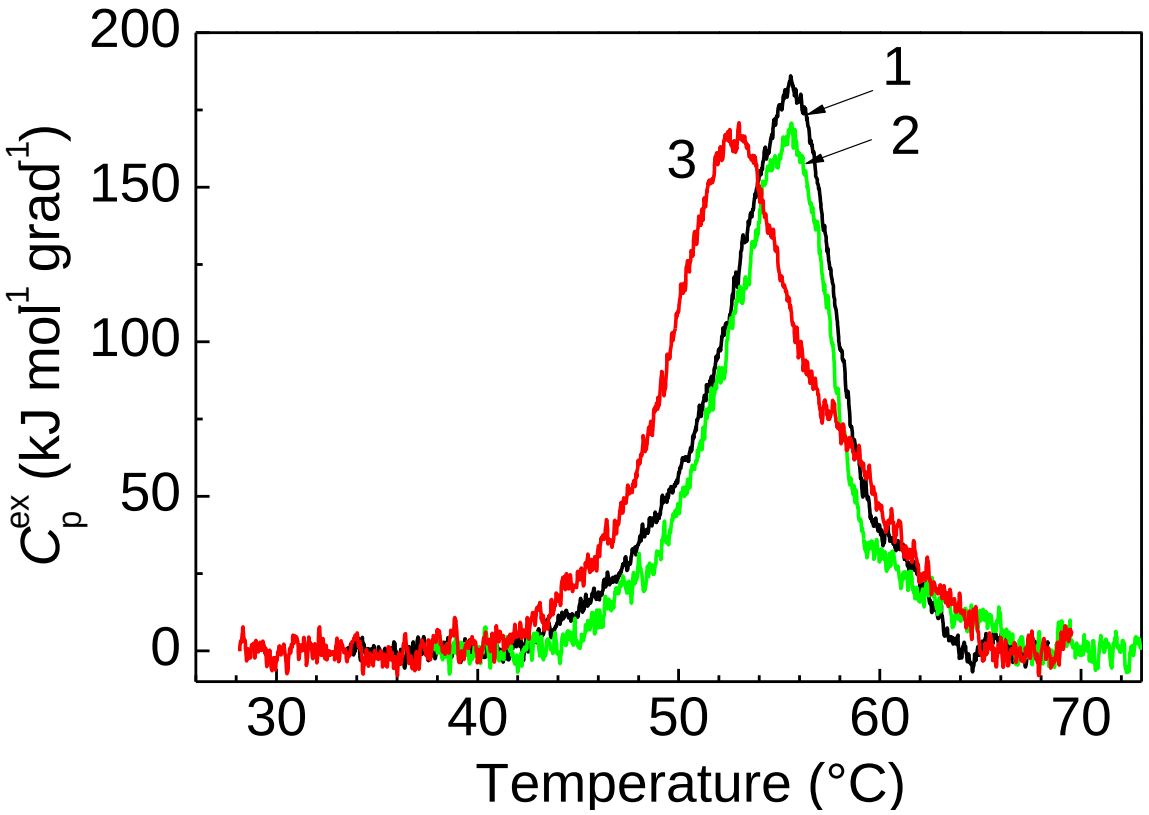

Effect of 2-hydroxypropyl-β-cyclodextrin (HP-β-CD) on thermal denaturation of glyceraldehyde-3-phopshate dehydrogenase (0.4 mg/mL; 2.8 μM).

Differential scanning calorimetry profiles were obtained at the following concentrations of HP-β-CD: 0 (1), 4 (2) and 76 mM (3). The heating rate was 1 °C/min.

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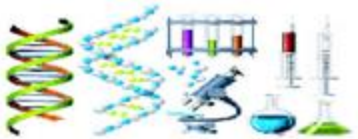

3. B.I.Kurganov and coworkers are the first to apply the test systems based on aggregation of UV-irradiated proteins for the quantitative estimation of the efficiency of aggregation suppressors (Muranov K.O., Maloletkina O.I., Poliansky N.B., Markossian K.A., Kleymenov S.Y., Rozhkov S.P., Goryunov A.S., Ostrovsky M.A., Kurganov B.I., Exp. Eye Res., 2011, v. 92, p. 76-86; Maloletkina O.I., Markossian K.A., Chebotareva N.A., Asryants R.A., Kleymenov S.Y., Poliansky N.B., Muranov K.O., Makeeva V.F., Kurganov B.I., Biophys. Chem., 2012, v. 163-164, p. 11-20; Roman S.G., Chebotareva N.A., Eronina T.B., Kleymenov S.Yu., Makeeva V.F., Muranov K.O., Poliansky N.B., Kurganov B.I., Biochemistry, 2011, v. 50, p. 10607-10623; Roman S.G., Chebotareva N.A., Kurganov B.I., Int. J. Biol. Macromol., 2012, v. 50, p. 1341-1345). The advantage of such test systems is the fact that they allow studying the effect of different agents on only one stage of the process, namely the stage of protein aggregation. As for the usual test systems based on thermal or dithiothreitol-induced aggregation of proteins as well as aggregation accompanying protein refolding, the total effect of the agents under study includes their action both on the stages of protein aggregation and the stages of the formation of intermediates prone to aggregation (for example, the stage of protein unfolding).

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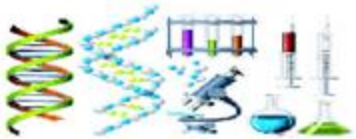

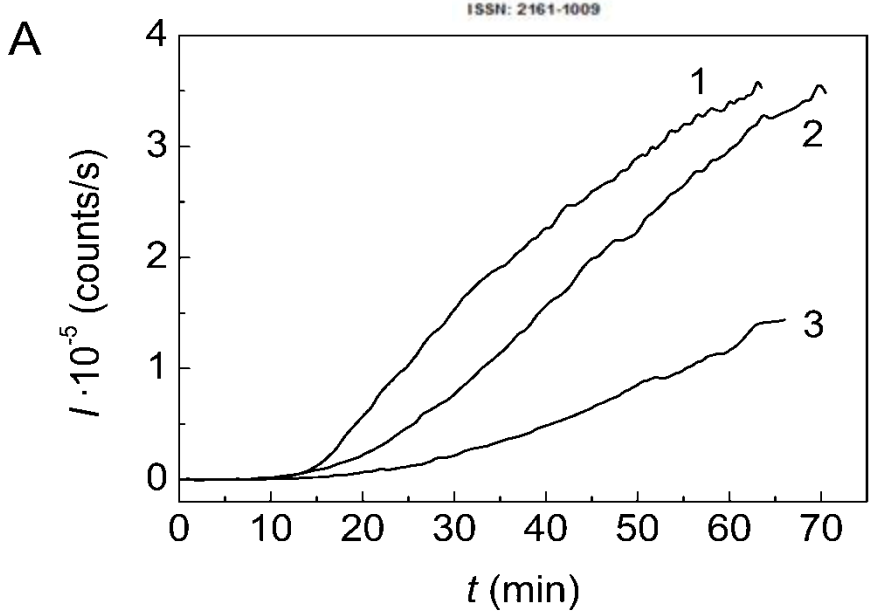

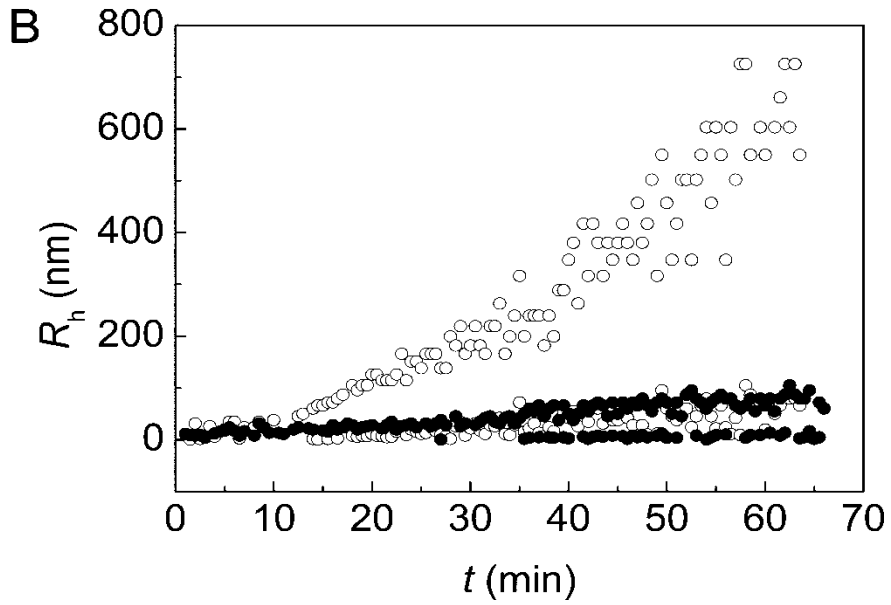

Aggregation of UV-irradiated glyceraldehyde-3-phopshate dehydrogenase (0.4 mg mL^{-1}; UV dose of 60 J cm^{-2}) at 37 °C in the presence of α-crystallin (50 mM phosphate buffer, pH 7.5).

(A) Dependences of the light scattering intensity (*I*) on time. The concentrations of α-crystallin were the following: (1) 0, (2) 0.025 and (3) 0.05 mg mL^{-1}.

(B) Dependences of the hydrodynamic radius (R_h) of protein aggregates obtained in the absence (open circles) or in the presence of 0.05 mg mL^{-1} of α-crystallin (solid circles).

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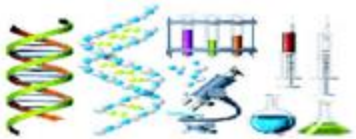

4. When registering aggregation of a target-protein by increase in the light scattering intensity, the diminishing of the anti-aggregation activity of alpha-crystallin (a representative of the family of small heat shock proteins) was observed under crowding conditions. The complexes of dissociated forms of alpha-crystallin with a target-protein resistant to aggregation in the presence of crowding agents were detected using analytical ultracentrifugation and size exclusion chromatography. B.I.Kurganov and coworkers have suggested that it has been just the complexes of dissociated forms of small heat shock proteins with non-native proteins which are responsible for the anti-aggregation activity of small heat shock proteins in the cell (Roman S.G., Chebotareva N.A., Eronina T.B., Kleymenov S.Yu., Makeeva V.F., Muranov K.O., Poliansky N.B., Kurganov B.I., Biochemistry, 2011, v. 50, p. 10607-10623; Kurganov B.I., Chebotareva N.A., Biochem. Anal. Biochem., 2013, v. 2, e138).

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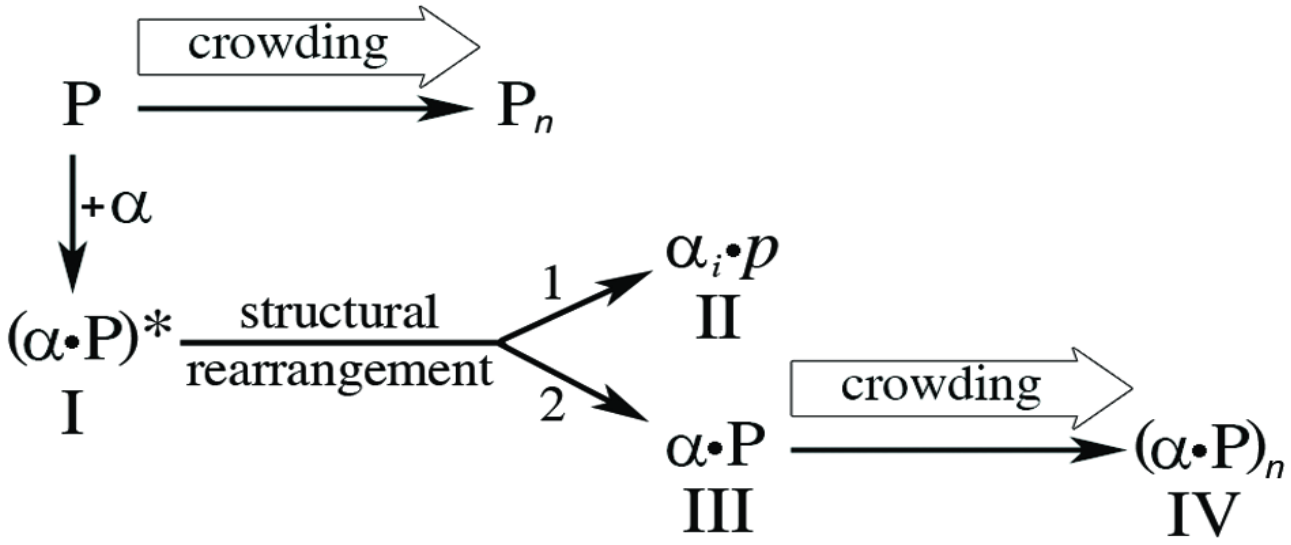

Scheme illustrating interaction of α-crystallin with a target protein under crowding conditions.

The addition of α-crystallin (α) to the protein substrate, (UV-irradiated Ph*b*; P), results in relatively fast formation of (α·P)* complex (complex I). Because of high mobility of α-crystallin particle complex I is very unstable and undergoes structural rearrangement which ultimately results in the formation of complex containing dissociated forms of α-crystallin, α_i, and dissociated forms of protein substrate, *p* (this complex α_i·*p* is designated as a complex II), and water soluble α-crystallin-unfolded target protein high molecular weight complex α·P (complex III). The complexes of the first type (complexes II) reveal a low propensity to aggregation even under crowding conditions. The complexes of the second type (complexes III) are characterized by the lower rate of aggregation in comparison with original UV-irradiated Ph*b*. However, crowding stimulates aggregation of these complexes resulting in a decrease in the chaperone-like activity of α-crystallin registered by the measurement of the increment of the light scattering intensity.

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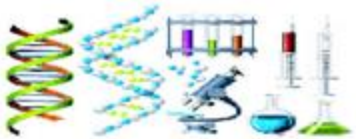

5. The new methods for analysis of the dependences of the initial rate of target-protein aggregation on the concentration of protein or chemical chaperone have been proposed (Chebotareva N.A., Eronina T.B., Roman S.G., Poliansky N.B., Muranov K.O., Kurganov B.I., Int. J. Biol. Macromol., 2013, v. 60, p. 69-76; Borzova V.A., Markossian K.A., Kara D.A., Chebotareva N.A., Makeeva V.F., Poliansky N.B., Muranov K.O., Kurganov B.I., PLoS One, 2013, v. 8, e74367; Kurganov B.I., Biochem. Anal. Biochem., 2013, v. 2, e136; Kurganov B.I., Biochemistry (Moscow), 2013, v. 78, No. 13, p. 1554-1566; Eronina T.B., Chebotareva N.A., Roman S.G., Kleymenov S.Yu., Makeeva V.F., Poliansky N.B., Muranov K.O., Kurganov B.I., Biopolymers, 2014, v. 101, p. 504–516). These methods allow calculating the adsorption capacity (AC) of protein chaperone with respect to a target-protein and affinity of chemical chaperone with respect to a target-protein expressed as a semi-saturation concentration ($[L]_{0.5}$). Parameters AC and $[L]_{0.5}$ can be used for characterization of anti-aggregation activity of protein and chemical chaperones, respectively.

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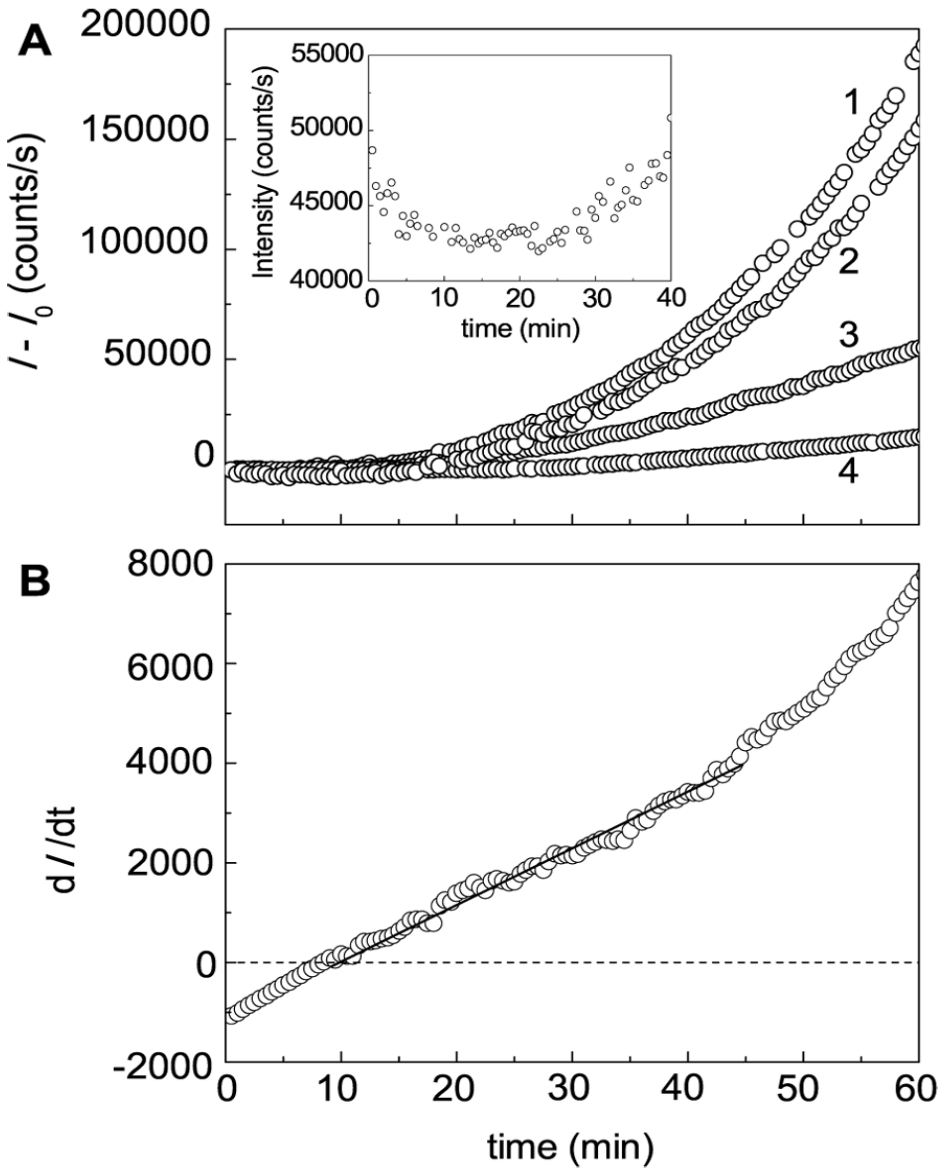

Effect of α-crystallin on dithiothreitol-induced aggregation of bovine serum albumin (0.1 M phosphate buffer, pH 7.0; 45 °C) .

A) The dependences of the light scattering intensity on time obtained at the following concentrations of α-crystallin: (1) 0, (2) 0.01, (3) 0.1 and (4) 1 mg/ml ([BSA] = 1.0 mg/ml; 2 mM DTT; 0.1 M phosphate buffer, pH 7.0; 45 °C). I and I_0 are the current and initial values of the light scattering intensity, respectively. The inset shows the dependence of I on time obtained at the concentration of α-crystallin 0.5 mg/ml. B) The dependence of dI/dt on time at α-crystallin concentration of 0.05 mg/ml. Points are the experimental data. The solid curve was calculated from the equation: $dI/dt = 2K_{agg}(t - t_0)$, where K_{agg} is a parameter characterizing the initial rate of aggregation and t_0 is the length of the lag period.

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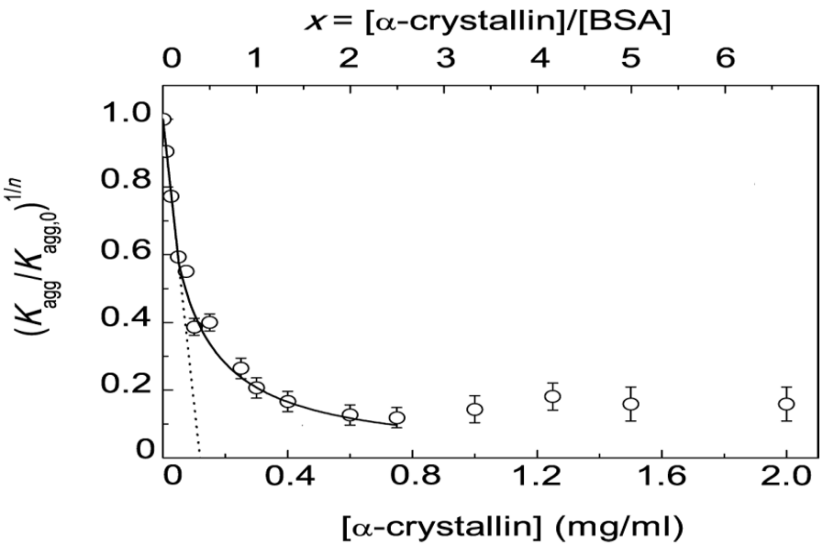

Initial rate of dithiothreitol-induced aggregation of bovine serum albumin as a function of α-crystallin concentration (45 °C; 2 mM DTT).

The dependence of $(K_{agg}/K_{agg,0})^{1/n}$ on α-crystallin concentration (lower abscissa axis) or the ratio of the molar concentrations of α-crystallin and BSA (upper abscissa axis x = [α-crystallin]/[BSA]; the order of aggregation with respect to the protein n = 1.6). Points are the experimental data. The initial part of the dependence of $(K_{agg}/K_{agg,0})^{1/n}$ on x follows the equation: $(K_{agg}/K_{agg,0})^{1/n} = 1 - AC_0x$, where AC_0 is the adsorption capacity of chaperone with respect to a target-protein. AC_0 = 2.5 BSA molecules per one subunit of α-crystallin.

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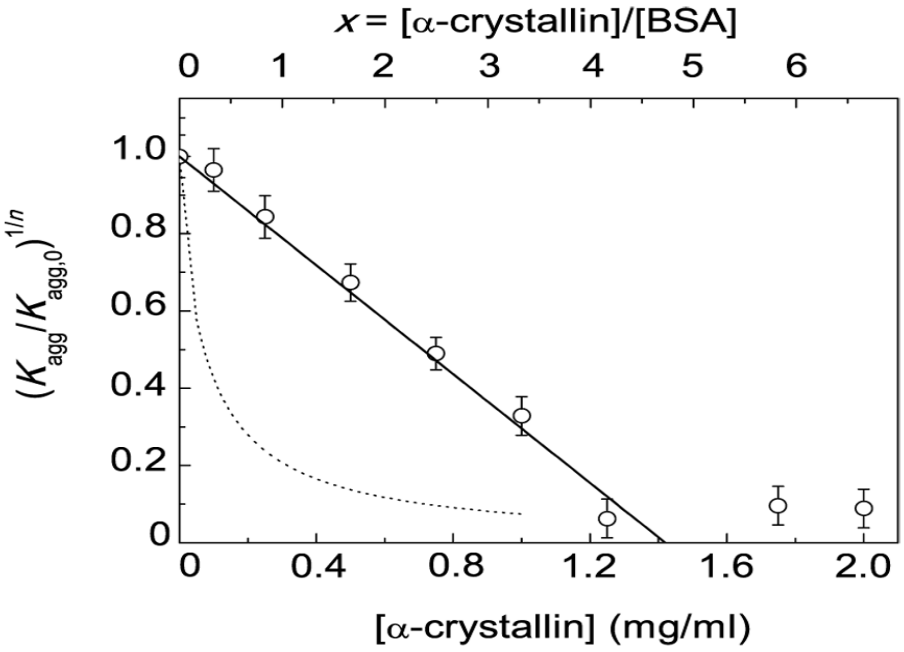

Initial rate of dithiothreitol-induced aggregation of bovine serum albumin at 45 °C as a function of cross-linked α-crystallin concentration.

The solid line was calculated from the equation $(K_{agg}/K_{agg,0})^{1/n} = 1 - AC_0x$ at $AC_0 = 0.21$ BSA molecules per one subunit of α-crystallin. The dotted line corresponds to the dependence of $(K_{agg}/K_{agg,0})^{1/n}$ on concentration of intact α-crystallin ($n = 1.6$).

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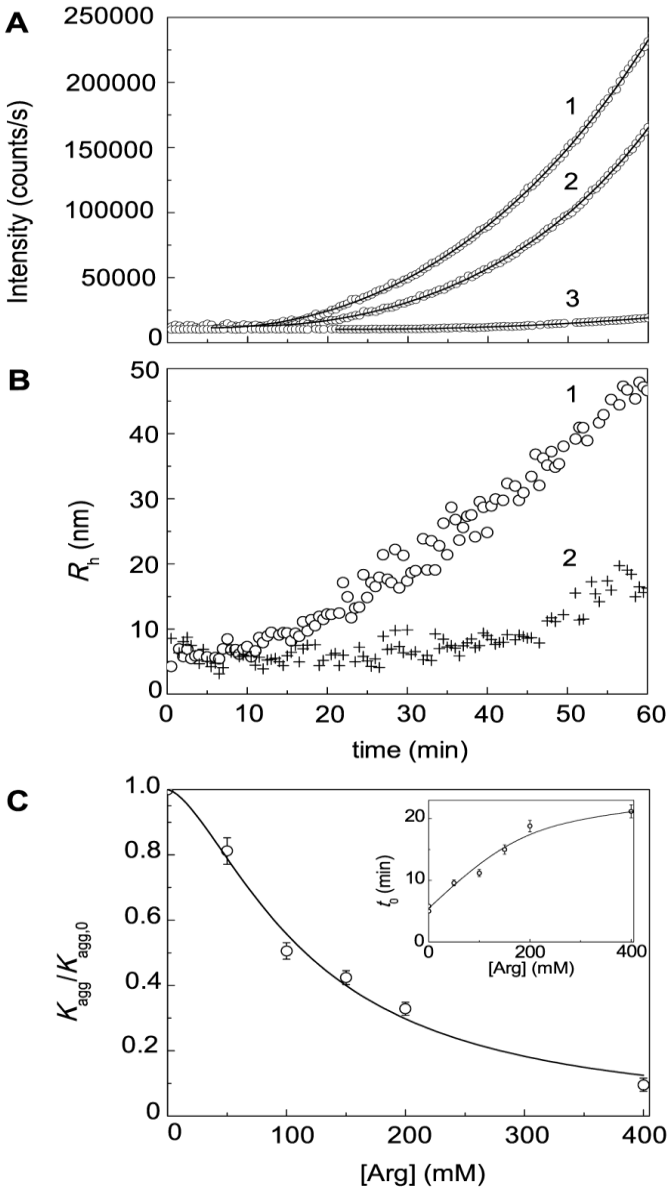

Effect of arginine (Arg) on dithiothreitol-induced aggregation of bovine serum albumin ([BSA] = 1.0 mg/ml, 2 mM DTT).

(A) The dependences of the light scattering intensity on time obtained at the following concentrations of Arg: (1) 0, (2) 50 and (3) 400 mM. Points are the experimental data. The solid curves was calculated from the equation: $I = K_{agg}(t - t_0)^2$ (K_{agg} is a parameter characterizing the initial rate of aggregation and t_0 is the length of the lag period).

(B) The dependences of the hydrodynamic radius (R_h) of the protein aggregates on time obtained in the absence of Arg (1) and in the presence of 400 mM Arg (2).

(C) The dependence of the $K_{agg}/K_{agg,0}$ ratio on the concentration of Arg. Points are the experimental data. The solid curve was calculated from the equation: $K_{agg}/K_{agg,0} = 1/\{1 + ([L]/[L]_{0.5})^h\}$, where $[L]_{0.5}$ is the semi-saturation concentration and h is the Hill coefficient. $[L]_{0.5}$ = 116 mM, h = 1.6. Inset shows the dependence of the length of the lag period (t_0) on the concentration of Arg.

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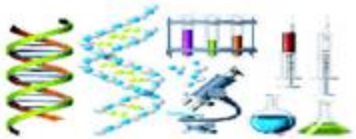

6. Investigations of reconstruction of holoform of glycogen phosphorylase *b* from apophosphorylase and cofactor (pyridoxal-5'-phosphate) allow putting forward an idea on a new physiological function of chaperones. This function consists in acceleration of reconstruction of holoenzyme by counteracting apoenzyme self-association that becomes especially significant under crowding conditions (Chebotareva N.A., Eronina T.B., Roman S.G., Poliansky N.B., Muranov K.O., Kurganov B.I., Int. J. Biol. Macromol., 2013, v. 60, p. 69-76).

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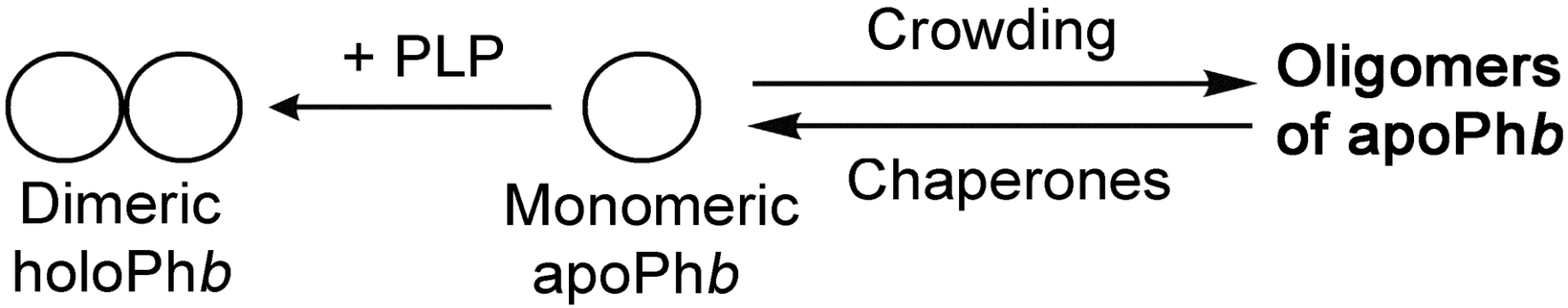

The scheme illustrating a new physiological function of chaperones.

Chaperones facilitate reconstitution of apoenzyme by preventing its self-association. ApoPh*b* and holoPh*b* are the apo- and holoforms of glycogen phosphorylase *b*, respectively.

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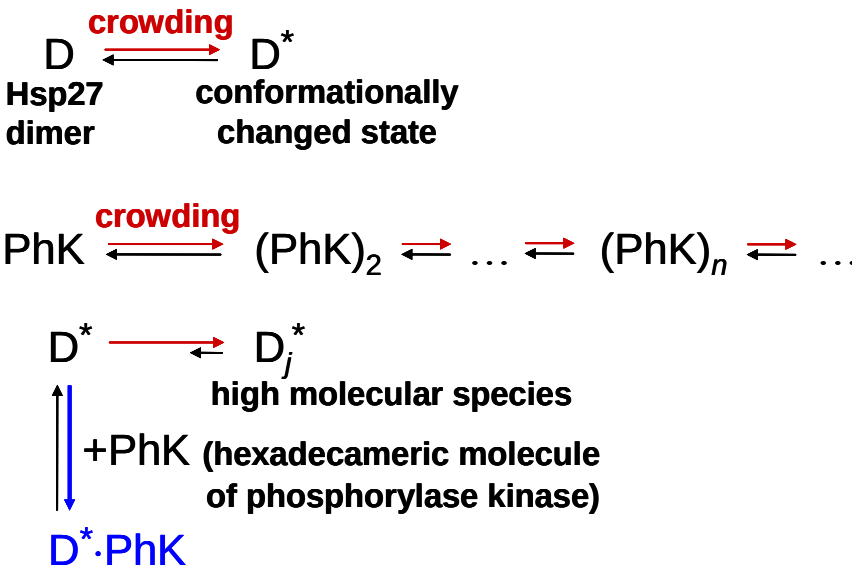
7. A hypothesis for participation of phosphorylase kinase in regulation of chaperone capacity of the cell was put forward on the basis of experimental data demonstrating interaction between native phosphorylase kinase and small heat shock proteins (Hsp27 and alpha-crystallin) under crowding conditions (Chebotareva N.A., Makeeva V.F., Bazhina S.G., Eronina T.B., Gusev N.B., Kurganov, B.I. Macromol. Biosci., 2010, v. 7, p. 783-789).

Interaction of the wild type (wt) heat shock protein Hsp27 and its 3D mutant (mimicking phosphorylation at Ser15, 78 and 82) with rabbit skeletal muscle phosphorylase kinase (PhK) was studied under crowding conditions modeled by addition of 1 M trimethylamine N-oxide. According to the data of sedimentation velocity and dynamic light scattering crowding provokes formation of high molecular mass associates of both PhK and Hsp27. Under crowding conditions small molecular mass associates of PhK and Hsp27 interact with each other thus leading to dissociation of large homooligomers of each protein. Taking into account high concentrations of PhK in the cell, we suppose that native PhK might modulate the oligomeric state and chaperone-like activity of Hsp27.



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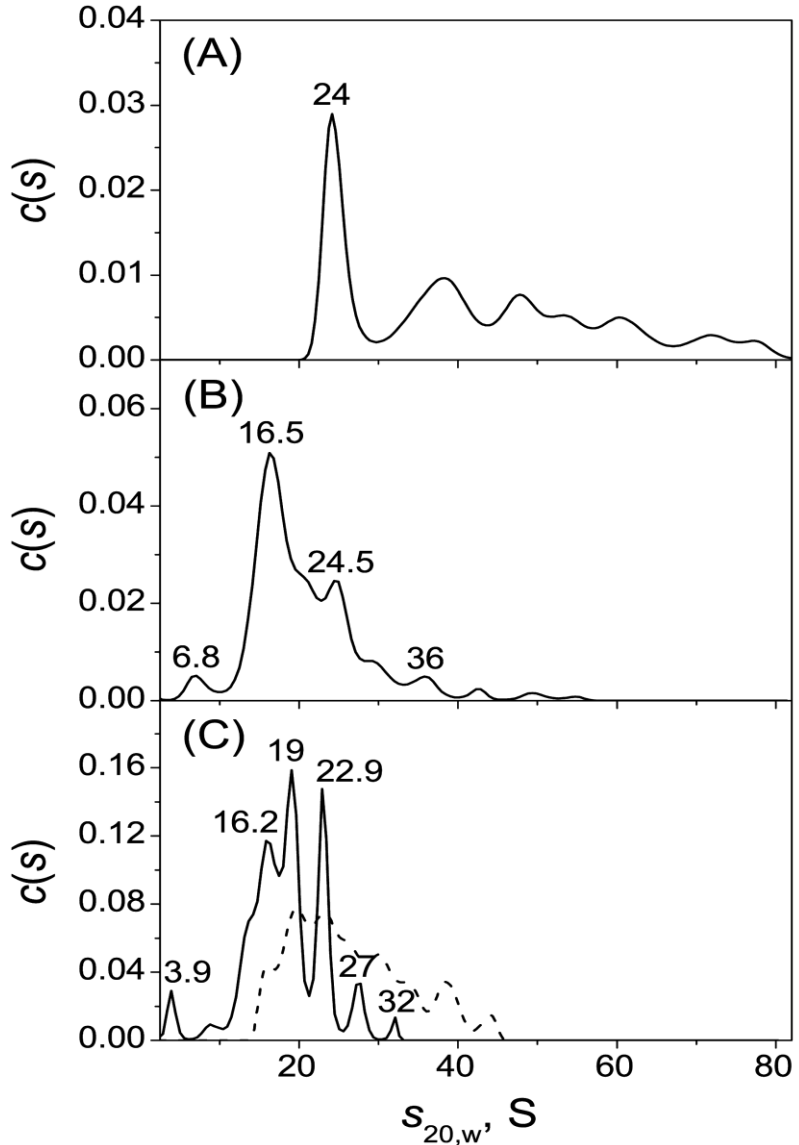

Interaction of PhK with the wt-Hsp27 under crowding conditions (1 M TMAO) at 20 °C (40 mM Hepes buffer, pH 6.85, containing 0.1 M NaCl, 0.1 mM $CaCl_2$ and 10 mM $MgCl_2$).

c(*s*) distribution for PhK (0.3 mg·mL^{-1}; A) and its mixtures with wt-Hsp27 (0.15 mg·mL^{-1}; B and 0.3 mg·mL^{-1}; solid curve in panel C). Dashed curve in the panel C represents *c*(*s*,*) distribution of the wt-Hsp27 (0.3 mg·mL^{-1}). Rotor speed 34 000 rpm.

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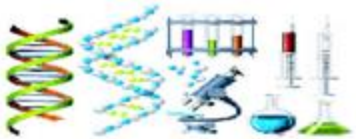

8. The effects of arginine on protein-protein interactions have been studied using phosphorylase kinase (PhK) from rabbit skeletal muscles as an example (Eronina T.B., Chebotareva N.A., Sluchanko N.N., Mikhaylova V.V., Makeeva V.F., Roman S.G., Kleymenov S.Y., Kurganov B.I., Int. J. Biol. Macromol., 2014, v. 68, p. 225-232). PhK, a 1.3 MDa $(\alpha\beta\gamma\delta)_4$ hexadecameric complex, is a Ca^{2+}-dependent regulatory enzyme that catalyzes phosphorylation and activation of glycogen phosphorylase *b*. On the basis of light scattering measurements it was shown that arginine induced aggregation of Ca^{2+}-free PhK. On the contrary, when studying Ca^{2+}, Mg^{2+}-induced aggregation of PhK at 37 °C, the protective effect of arginine was demonstrated. The data on analytical ultracentrifugation are indicative of disruption of PhK hexadecameric structure under the action of arginine. Though HspB6 and HspB5 suppress aggregation of PhK, they do not block the disruption effect of arginine with respect to both forms of PhK (Ca^{2+}-free and Ca^{2+}, Mg^{2+}-bound conformers). The dual effect of arginine has been interpreted from view-point of dual behaviour of arginine, functioning both like an osmolyte and a protein denaturant.

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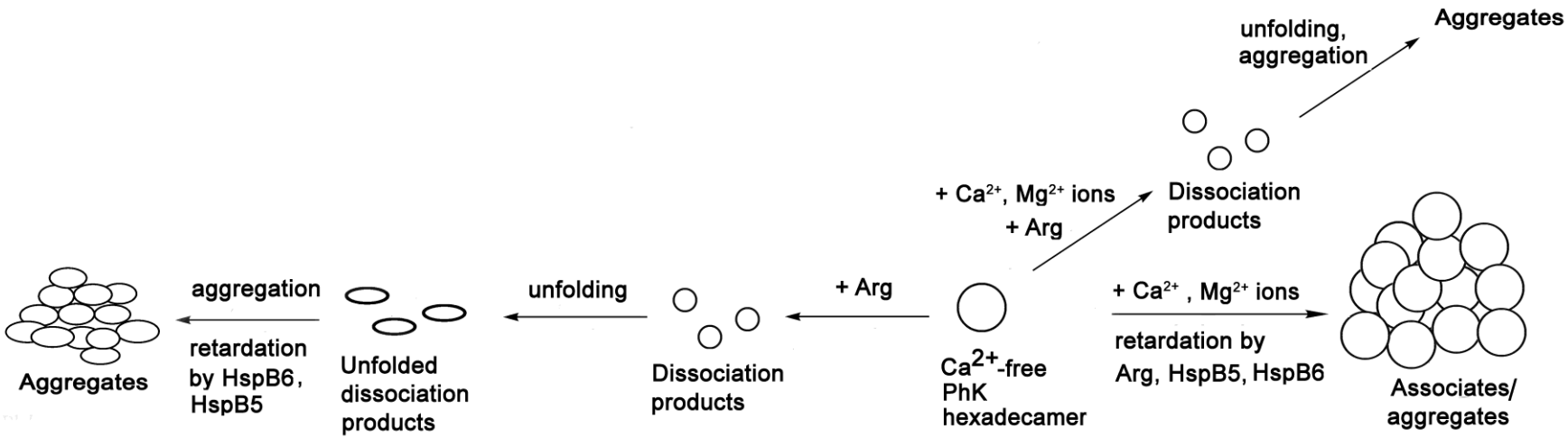

Dual effect of arginine (Arg) on aggregation of phosphorylase kinase (PhK) from rabbit skeletal muscles.

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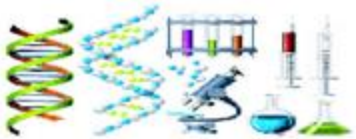

The agents exhibiting anti-aggregation activity can be applied in biotechnological productions, in particular, for stabilization of protein preparations and for facilitation of refolding of recombinant proteins, as well as for design of medicinal drugs intended for the treatment of neurodegenerative and other diseases caused by accumulation of protein aggregates in the cell.

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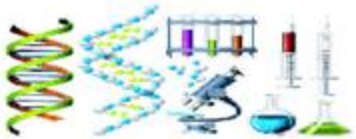

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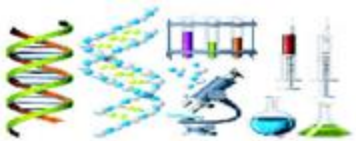

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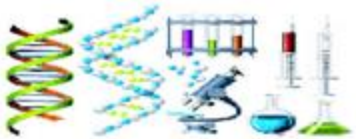

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