Crystal Structure of the C-terminal 10-kDa Subdomain of Hsc70*

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The 70-kDa heat shock proteins (Hsp70), including the cognates (Hsc70), are molecular chaperones that prevent misfolding and aggregation of polypeptides in cells under both normal and stressed conditions. They are composed of two major structural domains: an N-terminal 44-kDa ATPase domain and a C-terminal 30-kDa substrate binding domain. The 30-kDa domain can be divided into an 18-kDa subdomain and a 10-kDa subdomain. Here we report the crystal structure of the 10-kDa subdomain of rat Hsc70 at 3.45 Å. Its helical region adopted a helix-loop-helix fold. This conformation is different from the equivalent subdomain of DnaK, the bacterial homologue of Hsc70. Moreover, in the crystalline state, the 10-kDa subdomain formed dimers. The results of gel filtration chromatography further supported the view that this subdomain was self-associated. Upon gel filtration, Hsc70 was found to exist as a mixture of monomers, dimers, and oligomers, but the 60-kDa fragment was predominantly found to exist as monomers. These findings suggest that the α-helical region of the 10-kDa subdomain dictates the chaperone self-association.

Members of the 70-kDa heat shock protein family (Hsp70), including the cognate (Hsc70), are ATP-dependent molecular chaperones that play an essential role in many cellular processes (1, 2). Biochemical studies clearly demonstrate that Hsc70 is composed of at least two structural domains. The N-terminal 44-kDa domain contains a nucleotide binding site and possesses a weak intrinsic ATP-hydrolytic activity (3–5). The C-terminal 30-kDa domain has the capacity to bind unfolded polypeptides (6). Binding of peptides frequently leads to a stimulation of ATP hydrolysis by Hsc70 (5, 7). Moreover, peptide affinity for hsc70 is relatively high in the ADP-bound state but reduced in the ATP-bound state (8, 9). Thus, the activities of these two domains are coupled. It has also been shown that the 30-kDa domain can be further divided into N-terminal 18-kDa and C-terminal 10-kDa subdomains. Although the 18-kDa subdomain contains the binding site for peptides (10, 11), the 10-kDa subdomain is necessary for maintaining the peptide-bound state (6). Several atomic resolution structures of the domains of Hsc70 and DnaK (an Hsc70 homologue in bacteria) have been reported. The N-terminal 44-kDa domain comprises two major lobes whose interface forms a deep cleft for binding of ATP or ADP (4). The C-terminal 18-kDa subdomain consists of a β-sandwich, whereas the 10-kDa subdomain is predominantly α-helical (12–15). The last 30–40 amino acids at the C terminus have not been resolved, conceivably because of high flexibility. Nevertheless, this C-terminal tail of most, if not all, eukaryotic Hsc70 is conserved, containing GGX repeat and an EEVD motif (1). Hsc70 must work with other proteins to carry out its diverse cellular functions. In several cases, the sites on hsc70 responsible for the protein-protein interactions have been identified. For instance, the N-terminal 44-kDa domain interacts with both Hsp70-interacting protein (Hip) (16) and Bel-2-binding anathagene (BAG-1) (17, 18). The C-terminal 10-kDa subdomain appeared to interact with Hdj-1/Hsp40 (19), and the PTIEVD sequence at the C terminus is responsible for interacting with a group of tetratricopeptide repeat-containing proteins (20–22). Therefore, although the C-terminal tail of hsc70 is highly flexible, it plays important functional roles through interacting with specific target proteins. Moreover, the 30-kDa domain has been shown to be responsible for chaperone self-association (23–25). It nevertheless remains controversial as to whether the 18-kDa subdomain or the 10-kDa subdomain is critical for this phenomenon (24, 25). To gain insight into the structure-function relationship of the 10-kDa subdomain, we have determined its crystal structure from rat Hsc70. The polypeptide adopted a conformation significantly different from that of the equivalent subdomain in DnaK. Our results also demonstrated that the 10-kDa subdomain played a dominant role in the self-association of Hsc70.

MATERIALS AND METHODS

Preparation of Selenomethionine-incorporated 10-kDa Subdomain—Construction of the plasmid pCT10/R, suitable for expressing the 10-kDa subdomain (amino acids 542–646) of rat Rattus norvegicus Hsc70, was described previously (6). The recombinant protein was purified using the Fast-flow nickel-nitrilotriacetic acid resin (Qiagen). For the production of a selenomethionine-incorporated 10-kDa subdomain, the plasmid pCT10/R was transformed into Escherichia coli BL834(DE3) (Novagen), and the transformants were grown in the LeMaster medium (26). The molecular masses of wild-type and selenomethionine-labeled polypeptides were subsequently determined using a Bio-Q electrospray ionization mass spectrometer (Micromass). The results indicated that four methionine residues were fully substituted by selenomethionine (data not shown).

Crystallization and Data Collection—The purified selenomethionine-incorporated 10-kDa subdomain, including the N-terminal His tag portion, was crystallized as described (27). Crystals were grown by the hanging-drop vapor diffusion method from solutions containing ammonium sulfate as precipitant. The crystals belong to space group P6122 with cell dimensions of a = b = 119.0 Å, c = 166.4 Å, and there are four molecules per asymmetric unit.

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MAD1 data for selenomethionine-labeled polypeptides were collected at the BL18B synchrotron beam line of Photon Factory (in High Energy Accelerator Organization), Tsukuba, Japan. A single crystal was frozen at 110 K using paratone-N (Hampton Research) as cryoprotectant. MAD data was collected at four wavelengths. Two wavelengths were chosen near the absorption peak and the edge of selenium, 0.9793 and 0.9795 Å, corresponding to the maximum $\frac{f}{H_{11033}}$ and the minimum $\frac{f}{H_{11032}}$, respectively. Two remote energies were selected as references with wavelengths of 0.9400 and 0.9801 Å, respectively. Four sets of data were collected using Quantum 4R CCD detector and the implemented software for monitoring the experimental conditions. All data sets were obtained from a single crystal and then were indexed and integrated using DPS/MOSFLM (28) followed by scaling with SCALA (29). The structure-factor amplitudes were calculated using TRUNCATE (29). The statistics of MAD data are shown in Table I.

### Table I

| Wavelength (Å) | $\lambda_{1}$ min $f'$ | $\lambda_{2}$ max $f'$ | $\lambda_{3}$ remote1 | $\lambda_{4}$ remote2 |
|----------------|------------------------|------------------------|-----------------------|-----------------------|
| 0.9795         | 0.9793                 | 0.9400                 | 0.9802                |
| 3.45           | 3.45                   | 3.45                   | 3.45                  |
| 9136           | 9139                   | 9124                   | 9131                  |

| Completeness (%) |
|------------------|
| Overall          | 98.7                 | 98.7                   | 98.8                  | 98.8                  |
| Outermost shell  | 98.8                 | 98.9                   | 98.7                  | 98.7                  |
| $R_{merge}$ (%)  |
| Overall          | 8.2 (18.5)           | 8.4 (19.0)             | 8.5 (21.0)            | 7.9 (20.5)            |
| (I/|Ihkl|)               |
| 5.4              | 6.4                   | 5.8                    | 5.8                   |

### Refinement

| Resolution range (Å) |
|----------------------|
| 14.93–3.45           |
| R/|Rfree| |
| 24.9/30.7            |
| Protein atoms        |
| 2682                 |
| Solvent atoms        |
| 23                   |
| Overall $R$ value ($Å^2$) |
| 45.8                 |
| r.m.s. difference of bond lengths (Å) |
| 0.009                |
| r.m.s. difference of bond angles (degrees) |
| 1.4                  |

- $R_{merge} = \sum_{hkl} |I_{hkl}-\langle I_{hkl}\rangle|/\sum_{hkl} I_{hkl}$
- The number in parentheses is for the outermost shell.

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**Sequence comparison.** Aligned amino acid sequences of the 10-kDa subdomain for several eukaryotic Hsc70s and DnaK. Identical and similar residues are highlighted in orange and yellow, respectively. The secondary structural (s.s.) elements of DnaK are shown in blue, and those of rat Hsc70, obtained from this study, are in red. The GenBank™ accession numbers for rat, bovine, human, Drosophila melanogaster, and Saccharomyces cerevisiae are AAA41354, P19120, P08107, and AAB59186, respectively.

**Fig. 1.** Sequence comparison. Aligned amino acid sequences of the 10-kDa subdomain for several eukaryotic Hsc70s and DnaK. Identical and similar residues are highlighted in orange and yellow, respectively. The secondary structural (s.s.) elements of DnaK are shown in blue, and those of rat Hsc70, obtained from this study, are in red. The GenBank™ accession numbers for rat, bovine, human, Drosophila melanogaster, and Saccharomyces cerevisiae are AAA41354, P19120, P08107, and AAB59186, respectively.
chemical sequence to the density of the side chains was begun first with the positioning of the eight clear density regions of selenomethionines. The weak side chains were tentatively assigned by alanine residues at this stage. The initial model consisted of the four molecules, A537–A620, B537–B618, C534–C621, D537–D614, and 23 water molecules. The remaining residues of the four molecules, A621–A646, B618–B646, C622–C646, and D615–D646, could not be traced due to their poor electron density maps. Residues preceding position 542 of each molecule are from the His tag. The current model has an R-factor of 24.9% for all reflections above 2σ between 15.0- and 3.45-Å resolution and an Rexplo of 30.7%, using 5% randomly distributed reflections. Analysis of the Ramachandran plot showed two violations of accepted backbone torsion angles, except for Asn-563 located at loop region of subunit B. HELIXANG and CONTACTS of the CCP4 suite were used to analyze properties of the helices and intermolecular interactions. Coordinates have been deposited in the Protein Data Bank under accession code 1UD0.

Preparation of the 60-kDa Fragment—Previously, a plasmid (pHsc70-Ct) suitable for the expression of the 60-kDa fragment of Hsc70 was constructed (11). To introduce a His tag at the C terminus of the polypeptide, we digested pHsc70-Ct with NdeI and Xhol. Then, the insert was isolated and ligated with pET-22b (Novagen) treated previously with these two restriction enzymes, resulting in p60K/22b. The plasmid was now used to express the 60-kDa fragment with six histidines at its C terminus. The expression and purification of the tagged protein was described previously (6). The purified 60-kDa fragment and bovine hsc70 (5) were used for gel filtration analysis, as shown in Fig. 4B.

Size-exclusion Chromatography—Size-exclusion chromatography was carried out at 4 °C using an AKTA-FPLC system (Amersham Biosciences). Hsc70 and the 60-kDa fragment in buffer A (0.1 M NaCl in 50 mM Tris-HCl, pH 7.9) were applied to a Superdex200 HR10/30 column (Amersham Biosciences) equilibrated with the same buffer. The columns were calibrated using a kit range with sizes ranging from 16.4 Å (13.7 kDa) to 85 Å (669 kDa).

RESULTS

Structures of the Four 10-kDa Subdomains in the Asymmetric Unit—The topology of four 10-kDa fragments, 10-kDa-A, 10-kDa-B, 10-kDa-C, and 10-kDa-D, in the asymmetric unit were essentially the same, They folded into a helix-loop-helix structure comprising an N-terminal short helix (αB′), a 10-residue loop (L), and a 70-A-long kink helix (αC) (Fig. 2A). The long helix of the four molecules is slightly kinked at two positions. For instance, the long helix of molecule A is bent 10° at Glu-588 and 32° at Val-602. The stability of each molecule was maintained by an intramolecular hydrogen bond between the Lys-550 of αB′ and the Asn-575 of αC, as well as van der Waals interactions. In 10-kDa-C, there is an additional intramolecular hydrogen bond between Glu-543 and Gln-585.

![Fig. 2. Ribbon drawings of the four 10-kDa subdomains in an asymmetric unit. A–C show the four molecules, two coiled coil-like dimers, and the cruciform tetrameric structure in an asymmetric unit, respectively. The 2Fobs − F, electron density map was superimposed on the final 10-kDa-A molecule displayed by Ca. The map is contoured at 1.0σ.](image-url)
The pairwise C/r.m.s. distance measurements of the four molecules indicated that there were some local conformational differences among the four molecules. Although the r.m.s. distance between 10-kDa-A and 10-kDa-B is 1.26 Å, those of others range from 1.64 Å to 1.91 Å. Moreover, the conformation of the loop (from Glu-554 to Asn-563) of 10-kDa-A is similar to that of 10-kDa-D. In contrast, the loops of 10-kDa-B and 10-kDa-C adopt different conformations. For 10-kDa-B, the r.m.s. distance of C/H in the loop region was greater than 2 Å, as compared with other molecules in the asymmetric unit, thereby having the most distinct structure (Fig. 2A). However, the GGX P repeats and the EEVD motif at the C terminus were poorly visible, despite the fact that they were present in the polypeptides in the crystalline state. Only the first four to seven residues of the GGX P repeats were visible in 10-kDa-A (residues 615–620), 10-kDa-B (residues 615–618), and 10-kDa-C (615–621). On the basis of the visible portion of the GGX repeats, the flexible tail in 10-kDa-B pointed toward a direction different from those of 10-kDa-A and 10-kDa-C (Fig. 2A). Nevertheless, comparison could not be made between the direction of the tails of Hsc70 and DnaK since the last 32 amino acids are not present in the structure of the 30-kDa domain of DnaK (12).

Dimer and Oligomer in Crystalline State—In the crystal of 10-kDa fragment, the four molecules form two pairs of dimers, A-B and C-D, respectively (Fig. 2B). The long helices of two interacting monomers wrapped around each other, forming an antiparallel coiled-coil-like structure (Fig. 2B). One salt bridge and six to seven hydrogen bonds are present in each dimer (Table II). They conceivably were responsible for the stabilization of the structures, although they vary from one molecule to another. For instance, in molecules A, B, and D, the Trp-580 was hydrogen-bonded with Gln-595 of the interacting molecule in the dimers, whereas the Trp-580 of 10-kDa-C located between two different dimers was hydrogen-bonded with Asp-572.

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of 10-kDa-A. Moreover, the Trp-580 of 10-kDa-D formed an additional hydrogen bond with the Glu-591 of 10-kDa-C. Clearly, the partially buried side chain of Trp-580 in 10-kDa subdomain provides structural evidence for what has been reported of Trp-580 in Hsc70 (31).

The two dimers in the asymmetric unit crossed each other such that they formed a cruciform structure (Fig. 2C). The tetrameric structure in the crystal was stabilized by the interactions of residues from molecule A with residues from the C-D dimer (Fig. 2C). There are four and five hydrogen bonds between 10-kDa-A and 10-kDa-C as well as between A and D, respectively (Table II). Also, residues at either end of the two interacting dimers were involved in interacting with other symmetric molecules in the unit cell. Consequently, the 48 molecules in the unit cell formed a loose channel with a diameter of 50 Å when viewed along the c axis (Fig. 3). However, the appearance of the channel in the crystal could be misleading since this empty space may be occupied by the unstructured tails of each 10-kDa subdomain.

Oligomerization of the 10-kDa Subdomain in Solution—

Since the structure implied that the 10-kDa subdomain could form dimers, it now needed biochemical verification to confirm that was the case. We carried out gel filtration chromatography on this 10-kDa subdomain, and the results revealed that several species did co-exist (Fig. 4A). We next undertook to determine whether the 10-kDa subdomain was necessary for self-association. Both Hsc70 and its 60-kDa fragment were subjected to gel filtration analysis. As shown in Fig. 4B, Hsc70 existed as multiple species in solution. Similar, if not identical, results have been obtained previously (32). However, the 60-kDa fragment was predominantly monomeric. Therefore, these results indicated that the 10-kDa subdomain played an important role in the self-association of Hsc70.

Structural Divergence between the Helical Regions of Hsc70 and DnaK—Comparison between the structures of the 10-kDa subdomain of Hsc70 and that of DnaK (12) was made; the results are shown in Fig. 5A. Evidently, the 10-kDa subdomain of Hsc70 adopted a conformation different from that of DnaK. Although the subdomain of Hsc70 was composed of two helices of αB’ and αC (Fig. 2), the equivalent region of DnaK was composed of four helices, αB-αE (12). This difference became more apparent when the Ca of both structures was superimposed on each other. As shown in Fig. 5A, the αB’ helix of Hsc70 superimposed relatively well on part of the αB helix of DnaK, but the αC helix of Hsc70 did not superimpose on αC-αE helices of DnaK at all.

We also modeled the 30-kDa domain of Hsc70 in its peptide-bound state (Fig. 5B). Although the helical subdomain of DnaK was different from that of Hsc70, certain salt bridges could be conserved. For instance, in DnaKconstitute a salt bridge between Asp-540 of αB and Arg-467 of the β-sandwich. In our model, Glu-543 (equivalent to Asp-540 in DnaK) at the 10-kDa subdomain formed a hydrogen bond with Arg-469 (equivalent to Arg-467 in DnaK) at the 18-kDa subdomain (Fig. 4B). Indeed, it has been shown that replacing Glu-543 with lysine in bovine Hsc70 results in a 4.5-fold increase in the rate of peptide release and that the mutant could not form stable complexes with the denatured staphylococcal nuclease (33). Similarly, mutation of Arg-469 in rat Hsc70 also brings about a faster release of bound peptides and causes the protein to lose its capacity to form tightly associated complexes with carboxymethyl-α-lactalbumin (34). Therefore, it is likely that the salt bridges between the 18-kDa and 10-kDa subdomains in Hsc70 are involved in the maintenance of the substrate-bound state of the protein.

Herein, we have solved the crystal structure of the 10-kDa C-terminal subdomain of rat Hsc70. Two major conclusions can be drawn from our study. The first conclusion is that the 18-kDa subdomain is predominant for the self-association of Hsc70. Contrary to our verdict, Fouchaq et al. (25) concluded that the 18-kDa subdomain is responsible for dimerization of Hsc70 because both the 60-kDa fragment and the 18-kDa subdomain appeared to have the capacity to self-associate. It might be possible that these polypeptides at high concentrations could form oligomers since the 18-kDa subdomain contains the peptide binding site (10, 14). Our result, however, is in agreement with that of Willbanks et al. (24). Using small angle x-ray scattering, they also demonstrated that the 18-kDa fragment is monomeric. In any event, it remains to be determined how dimerization leads to higher order oligomerization and what this self-association means in real life.

The second conclusion is that the structure of the 10-kDa subdomain of Hsc70 adopts a helix-loop-helix conformation and that this folding pattern differs from that of DnaK. There are several possible explanations for the observed difference in structures. In the first place, the sequence homology between these two 10-kDa subdomains is low. In particular, the region corresponding to the loop between αC and αD helices in DnaK is distinct. Therefore, different folding of the 10-kDa subdomains between Hsc70 and DnaK might be due to variations in the primary sequences. Secondly, in our structure, the 18-kDa subdomain was not included in crystallization. However, the DnaK fragment used for structure determination contains the 18-kDa subdomain, although it lacks the C-terminal flexible tail. Thus, one simple interpretation is that subdomains in isolation fold differently. Thirdly, the structure of DnaK represents the substrate-bound state of the chaperone. Since substrate binding causes Hsc70 to change from oligomer to monomer (32), the dimeric structure shown in this study might conceivably correspond to a substrate-free state. Therefore, it raises the possibility that refolding of the C-terminal helices is accompanied by the chaperone switching from monomer to dimer. Obviously, further experiments are required for verifying this hypothesis.

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