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Hereditary transmission Hereditary transmission chemical protection Physical and Tafi Melanosome Berson et al. Recombinant CsgA formed fibres after standing for 4 h. Amyloid formation by CsgA is apparently tightly controlled, as there are a number of proteins which interact in the assembly process and which are controlled by two operons. CsgB is thought to aid in the nucleation of the fibrils, and both proteins are stabilised by the lipoprotein CsgG Lofler et al. NMR spectroscopy Schwarz-Linek et al. It seems likely that this type of interaction occurs between curli amyloid and fibronectin. The fibronectin type III module has been found to assemble into amyloid fibres independently Litvinovich et al. Three yeast prions in *S. cerevisiae*. These cellular proteins participate in diverse cellular functions. Prion proteins can undergo a conformational change, which alters the function of the protein and consequently the phenotype of the cell. Hydrophobins found in most fungi Gebbink et al. Similarly, the filamentous bacteria *Streptomyces coelicolor* produces chaplins that are used to attach to hydrophobic surfaces in a similar manner to hydrophobins in fungi Rev Physiol Biochem Pharmacol Previously shown to produce fibrils, chaplin from *S. coelicolor*. Viral peptides also form amyloids Table 2. Perhaps the most significant recent development in amyloid research is the discovery of physiologically relevant amyloid proteins in human tissue Fowler et al. Melanosomes are highly abundant organelles generated in specialised cells within the skin and eyes Hearing ; Marks and Seabra and contain glycoprotein Pmel17, known to play a role in pigmentation Raposo and Marks It now seems likely that more proteins will be discovered that naturally form amyloid with physiological roles, and this is suggested by the finding of amyloid receptors such as RAGE receptors for advanced glycation end products Bamberger et al. These protective mechanisms within the cell suggest that amyloid proteins are physiologically relevant and that the cell has developed mechanisms to protect itself from its deleterious effects. Similarly, if amyloids were only present as the end point of slow, degenerative diseases, and not present in normal healthy physiology, it is logical to assume that there would be minimal evolutionary selection for these clearance mechanisms due to the often late-onset and mortality of these diseases. Experimental detection and study of the properties of intermediates in amyloid formation, difficult though it might be due to their transient nature and subsequent water-insolubility of products, can provide valuable insights to structural transitions involved, aggregation states 20 Rev Physiol Biochem Pharmacol Some of the most important studies on conformational transitions are now described. Helix-sheet folding There is tantalising evidence for a mechanistic role in amyloidogenesis of helical-containing intermediates, and several of the observations that support this are discussed below Kirkitadze et al. The polylysine model is a simpler system in many ways than an aggregating protein, with a single type of inter-residue interaction and no defined tertiary structure. Above this minimum chain length, the transition temperature decreased as the chain length increased. It was found that chain length had an effect on the secondary structure of the polypeptide chain. As the molecular weight of the polymer increased, peak shifts were observed and a new band appeared at 1640 cm^{-1} . It was suggested that this was due to the presence of two sub-populations of helices. The conclusion reached by Dzwolak et al. There are other reports of a transient increase in helical content of proteins immediately prior to formation of amyloid fibrils Kirkitadze et al. Apolipoprotein A-1 is made up of repeating amphiphilic helices, and a heptad repeat pattern similar to that seen for coiled-coil proteins. However, in aqueous buffer at neutral pH the protein has a random coil structure. At pH 3, there is a gain in structure, as the internal fluorescence shows the three Trp residues are in a hydrophobic pocket Andreola et al. CD studies show an acquisition of helical structure at lower pH. The protein is not, however, stable at pH 4, forming insoluble material after around 5 min, the process being one of intermolecular association and then precipitation. Helical intermediates have also been observed for fibril growth on surfaces. Hua and Weiss examined the mechanism of insulin fibril formation after thermal

denaturation in acidic solution using ultra-rapid ^1H NMR spectroscopy. The structure of the intermediates was also investigated prior to aggregation, utilising low insulin concentration and ionic strength to delay the onset of aggregation. Secondary structure alterations in monomers could be assigned to particular regions of the protein by the use of NMR spectroscopy. The process involved represented segmental rather than global unfolding, with some helical elements and long-range interactions maintained. The hypothesis that distorted helices play an essential role in amyloid formation can explain the seemingly paradoxical effects observed when the structure-stabilising solvent 2,2,2-trifluoroethanol TFE was added to aqueous solutions of proteins Chiti et al. Solvent conditions which lower the energy barrier to helix formation will facilitate fibril formation if, at the same time, the energy barrier for conversion of helical-containing intermediates to fibrils is not substantially increased. At intermediate TFE concentrations, shorter stretches of helical structure should be preferred. In a study of the dependence of aggregation and folding on residue sequence identity Chiti et al. In a sample of 1, non-redundant proteins from the Protein Data Bank PDB, differences were examined between experimentally determined secondary structures and those predicted by a secondary structure prediction algorithm. They found that 37 of the proteins 2. These came from a wide range of proteins, including single helical peptides and large globular proteins, that varied in their cellular location being nuclear, cytosolic, integral and peripheral membrane proteins and extracellular. The interactions in these regions were assessed by examining the solvent-accessible surface area of each residue in the discordant helix as determined by the neighbouring residues and comparing the values calculated for a Gly-XGly tripeptide. The helices fell into three categories. One group had helices that were almost completely buried. There were six helices in the third group that were exposed along their entire length. Three of those are known to be lipid-associated in their native environment. In two of the cases the discordant helices are used in the formation of oligomers, which would help to stabilise those regions. This lack of stabilising interactions likely contributes to the aggregation tendency of this peptide, whereas all the other examples identified would be stabilised by interaction with either protein or lipid environments. Several proteins, not previously identified as fibril-forming, were also detected such as coagulation factor XIII, a triacylglycerol lipase, and a transpeptidase. Subsequent investigations of coagulation factor XIII, the specific triacylglycerol lipase and transpeptidase in physiological-like solutions, did in fact show the formation of fibrils Kallberg et al. Independent support for this hypothesis can be drawn from results involving helix stabilisation in other peptides and the effect on amyloid formation. The addition of a single methyl group was sufficient to cause this change. Similarly, Tjernberg et al. Finally, an interesting NMR solution structure Coles et al. A key observation Coles et al. We discuss some evidence for this proposition below. The equilibrium between the two helical forms is clearly affected by the polarity of the solvent, with low polarity solvents favouring α -helicity Pengo et al. These changes in the N-terminal region caused a significant change in the secondary structure of the protein. Importantly, the new structure retains the same number of hydrogen bonds as the native structure. The single N11L mutant was able to adopt either structure. Recently, we investigated Y. Backbone residues sticks, sidechains lines, carbon light blue, nitrogen dark blue, hydrogens white and oxygen red. Figures generated using InsightII v. The unusual stabil- 26 Rev Physiol Biochem Pharmacol Arrows show the direction of change over time. Images taken from Singh et al. Fairlie, submitted, some spectra were removed for easy interpretation. Figures illustrated and modified with Prism4 version 4. This may be a factor in promoting aggregation. However, it seems likely that the folding pathway to amyloid could potentially be accessed by any protein structural motif as Fig. Importance of protein unfolding Since the formation of amyloid fibrils involves changes in secondary structure, an obvious question is whether this occurs through partially folded intermediates or randomly structured segments. Clues to the structure of partially folded intermediates have been provided by spectroscopic studies, by the effects of single residue mutations, and by varying conditions under which intermediates form. Pre-formed fibrils were unstable at the higher temperatures. They showed that although a partially folded intermediate state was indicated, this had the same secondary structure composition as the native apomyoglobin, and the authors concluded that, at least in this instance, the

precursors of amyloid structure were unfolded chain segments. In support of their argument, they noted that very short peptides and several polyamino acids have the capacity to form amyloid fibrils. Although not conclusive, this supports unfolded precursors being involved in amyloid formation, at least for these two examples. There are also indications that the so-called unfolded conformation may be a misnomer, in that there may actually be discernible structure present, biased towards extended main chain conformations, which would be able to undergo alignment into amyloid fibrils. *Rev Physiol Biochem Pharmacol* Mutations also affect the formation of intramolecular bonds in the protein as shown by the p53 RH mutant associated with adrenocortical carcinoma in children. This mutation disrupts the intermonomer salt bridge and, at least for a portion of the mutant proteins, results in partial destabilisation Galea et al. This principle was also shown by non-amyloidogenic endostatin, which was able to form amyloid fibrils by removing disulphide bond-forming cysteines He et al. The cause of protein destabilisation and unfolding resulting in acquired amyloidosis is less clear. It is generally accepted that an increase in sporadic mutations can cause proteins to misfold and form amyloid fibrils, but is also proposed that an increase in local protein concentration may result in amyloid formation as a result of molecular crowding. External factors such as pH or the presence of denaturing conditions can initiate destabilisation, and such stimuli within the cell might similarly cause destabilisation. Interestingly, structural analysis of this mutant showed a native-like folding intermediate, where the destabilised intermediate was very similar to the wild-type protein except for the perturbation of the edge of the strands Jahn et al. By unfolding, hydrophobic regions may become solvent-exposed, aromatic residues brought to the surface, and secondary structures, previously stabilised by tight packing and intramolecular interactions, could then be destabilised. Amyloid formation The formation of amyloid can be considered to involve 1 conformational changes away from the native state in key regions of a protein or peptide, 2 intermolecular interactions that result in aggregated intermediates and 3 further aggregation in three dimensions to produce growing fibrils. Initial aggregation The detection of monomeric or early aggregation states has been difficult experimentally due to their transitory nature, their presence at only low concentrations and usually in an ensemble of conformations, and the speed with which insoluble aggregates are formed especially when seeded. In recent years, however, some progress has been made in identifying these early aggregates, providing some information on the oligomerisation process. Most recently, atomic force microscopy 30 *Rev Physiol Biochem Pharmacol* Wang and Colon have investigated a non-amyloidogenic form of M. Similar studies have also been done on other known amyloidogenic proteins. Insulin has been shown to exist as stable dimers, tetramers and hexamers in the gas phase using nanoflow electrospray mass spectroscopy and at higher concentrations up to mers Nettleton et al. High-resolution atomic force microscopy at low pH has provided images of monomer and dimeric insulin Jansen et al.

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Chapter 6 : B. Sakmann (Author of Reviews of Physiology, Biochemistry and Pharmacology, Volume)

Delineating the exchanger's most important, common features, and concentrating particularly on its role in cell pH and volume regulation. Keywords Neuropeptide Neurotransmitter Opioid-Rezeptoren Zell-pH-Wert Zellvolumen biochemistry hormone neurons neuropeptides neurotransmitter opioid pharmacology physiology receptor research sympathetic nerve.