Volume 263, Issue 3, 1 November 1996, Pages 432-446

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Assembly of the Herpes Simplex Virus Capsid: Characterization of Intermediates Observed During Cell-free Capsid Formation

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https://doi.org/10.1006/jmbi.1996.0587

Abstract

The herpes simplex virus-1 (HSV-1) capsid is an icosahedral shell approximately 15 nm thick and 125 nm in diameter. Three of its primary structural components are a major capsid protein (VP5; coded by the UL19 gene) and two minor proteins, VP19C (UL38 gene) and VP23 (UL18 gene). Assembly of the capsid involves the participation of two additional proteins, the scaffolding protein (UL26.5 gene) and the maturational protease (UL26 gene). With the goal of identifying morphological intermediates in the assembly process, we have examined capsid formation in a cell-free system containing the five HSV-1 proteins mentioned above. Capsids and capsid-related structures formed during progressively longer periods of incubation were examined by electron microscopy of thin-sectioned specimens. After one minute, 90 minutes and eight hours of incubation

the structures observed, respectively, were partial capsids, closed spherical capsids and polyhedral capsids. Partial capsids were two-layered structures consisting of a segment of external shell partially surrounding a region of scaffold. They appeared as wedges or angular segments of closed spherical capsids, the angle ranging from less than 30Â° to greater than 270Â°. Partial capsids are suggested to be precursors of closed spherical capsids because, whereas partial capsids were the predominant assembly product observed after one minute of incubation, they were rare in reactions incubated for 45 minutes or longer. Closed spherical capsids were highly uniform in morphology, consisting of a closed external shell surrounding a thick scaffold similar in morphology to the same layers seen in partial capsids. In negatively stained specimens, closed spherical capsids appeared round in profile, suggesting that they are spherical rather than polyhedral in shape. A three-dimensional reconstruction computed from cryoelectron micro graphs confirmed that closed spherical capsids are spherical with T=16 icosahedral symmetry. The reconstruction showed further that, compared to mature HSV-1 capsids, closed spherical capsids are more open structures in which the capsid floor layer is less pronounced. In contrast to closed spherical capsids, polyhedral capsids exhibited distinct facets and vertices, indicating that they are icosahedral like the capsids in mature virions. Upon incubation *in vitro*, purified closed spherical capsids matured into polyhedral capsids, indicating that the latter arise by angularization of the former. Partial capsids, closed spherical capsids and polyhedral capsids were all found to contain VP5, VP19C, VP23, VP21 and the scaffolding protein; the scaffolding protein being predominantly in the immature, uncleaved form in all cases. Polyhedral capsids and closed spherical capsids were found to differ in Î»their sensitivity to disruption at 2Â°C. Closed spherical capsids were disassembled while polyhedral capsids were unaffected. Our results suggest that HSV-1 capsid assembly begins with the partial capsid and proceeds through a closed, spherical, unstable capsid intermediate to a closed, stable, icosahedral form similar to that found in the mature virion. Structures resembling HSV-1 partial capsids have been described as capsid assembly intermediates in *Salmonella typhimurium* bacteriophage P22. HSV-1 capsid maturation from a fragile, spherical state to a robust polyhedral form resembles the prohead maturation events undergone by dsDNA bacteriophages including

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Keywords

herpes simplex virus; capsid assembly; electron microscopy; scaffolding protein; procapsid

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