Title:	The DNA-binding protein HU is a molecular glue that attaches bacteria to extracellular DNA in biofilms
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Abstract:	In biofilms, bacteria that possess a negatively charged surface are embedded within a matrix of polymers consisting mainly of negatively charged extracellular DNA (e-DNA). In all likelihood, a multivalent positively charged substance, for example, a basic protein, exists within biofilms to neutralize charge-charge repulsions and act as a 'glue' attaching negatively charged bacteria to negatively charged e-DNA; however, no protein capable of doing so has yet been identified. We decided to investigate whether a highly abundant nucleoid-associated histone-like protein (HU) happens to be the glue in question. In recent years, HU has been shown to possess qualities that could be considered desirable in the proposed glue, for example, (a) availability in association with e-DNA; (b) multivalent DNA binding; (c) non-sequence-specific DNA-binding; (d) enhancement of biofilm formation upon exogenous addition, and (e) disruption of biofilms, upon removal by HU-cognate antibodies. Geometric considerations suggest that basic residues in HU's canonical and noncanonical DNA-binding sites can interact with sugar-linked terminal phosphates in lipopolysaccharide (LPS) molecules in bacterial outer membranes. Here, using genetic, spectroscopic, biophysical-chemical, microscopy-based, and cytometry-based experiments, we demonstrate that HU's DNA-binding sites also bind to LPS, that this facilitates DNA-DNA, DNA-LPS, and LPS-LPS interactions, and that this facilitates bacterial clumping and attachment of bacteria to DNA. Exogenous addition of HU to bacteria in (nonshaken) cultures is shown to cause cells to become engulfed in a matrix of DNA, potentially arising from the lysis of bacteria with vulnerable cell walls (as they strain to grow, divide, and move away from each other, in opposition to the accreting influence of HUs).
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