

Advances in the study of adhesion behavior between bacteria and material interfaces

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Abstract

In biomedical, industrial, and marine fields, interactions between bacteria and material interfaces are of great importance in biofilm formation, biofouling, the development of antimicrobial surface technologies, and the changing patterns of bacterial adhesion behavior on non-biological surfaces become a focus of research by researchers. Bacteria move from planktonic to adhesive behavior through near-interfacial sociological behavior, specificity (specific bacterial appendages such as hairs, flagella, curls, etc. that can bind to some chemicals on certain surfaces), non-specific interactions (van der Waals forces, electrostatic interactions, hydrophobic interactions or acid-base interactions) and surface mechanical induction, a process that the bacteria themselves can influence, the nature of the interfacial material and the environment. A variety of methods have been developed to measure cell adhesion. The continued development of atomic force microscopy (AFM) techniques provides a more advanced means of exploring bacterial-surface interactions and the various physicochemical properties of bacterial cells. Based on a large amount of literature research and tracking of related technological research developments, this paper mainly introduces the domestic and international research progress on the adhesion behavior between bacteria and material interfaces in detail from the aspects of adhesion mechanism, influencing factors, and testing methods, to provide a solid theoretical basis for further advancing the study of bacterial-interface adhesion and to get more scholars' attention.

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KEYWORDS: microorganisms; biofilm; adhesion mechanism; influencing factors; atomic force microscopy

1. INTRODUCTION

Surface adhesion of bacteria is a common natural phenomenon, and it has become more and more important to study the mechanism of bacterial adhesion to various surfaces in recent decades, because it involves various fields such as biomedicine, industry, ocean and environment^[1]. Bacterial adhesion is the first step in their colonization and forming biofilms, which are harmful to human life and industrial production, for example, leading to infection of medical implants, microbial-induced corrosion, pathogen-host cell interactions, periodontitis or dental caries, and contamination of food processing equipment^[2-3]. However, microbial adhesion may also be beneficial, for example, in the degradation of environmentally harmful chemicals in soil, treatment of wastewater and waste gases in bioreactors, agricultural applications of rhizobia, and polymer degradation^[4-9]. Bacteria achieve free-to-irreversible adhesion through specific interactions with material surfaces, non-specific physicochemical interactions, and surface mechanical induction^[10]. Biofilms are formed when bacteria aggregate together to form communities attached to solid surfaces and encapsulated in extracellular polysaccharide matrices. The development process is divided into initial reversible adhesion of bacteria, irreversible adhesion and biofilm growth, and maturation and diffusion phases^[11]. This highly complex process is influenced by the bacteria, the adherent material, and the surrounding environment^[12]. The formation of bacterial biofilms is one of the mechanisms by which bacteria adapt to their environment, and biofilms rely on their complex internal structure and colony regulation to achieve variability in the external environment and resistance to bacteriostatic drugs^[13-14]. In recent decades, biofilm removal has become a global challenge^[15], as biofilms, once formed, are difficult to eradicate and can easily cause persistent and widespread bacterial infections with severe consequences. The introduction of atomic force microscopy (AFM) techniques has led to a significant breakthrough in studying bacterial-material surface interactions, enabling the analysis of biofilm or single cell-material surface interactions^[16]. AFM can be operated in a liquid environment to study cells' mechanical properties and the biofilms' stiffness^[17]. Initial adhesion of free bacteria to the material surface is necessary for forming biofilms. The first approach to prevent the formation of biofilms on the material surface is to avoid the initial adhesion of bacteria. In this paper, we review the adhesion mechanism, influencing factors, and testing methods between bacteria and material interfaces to expand researchers' understanding of adhesion between bacteria and materials and provide directions for solving harmful adhesion of bacteria.

2. MECHANISM OF ADHESION OF BACTERIA TO MATERIAL SURFACES

2.1 The near-interface sociological behavior of bacteria

According to social-microbiology theory^[18], social behavior is performed by one individual. It impacts other individuals and consists of four main categories: self-interest, other-interest, double benefit, and double damage^[19]. It has been suggested that the microbial periplasm is similar to a human community, in which the extracellular polymer matrix (EPS) acts as the material base and forms the house's skeleton and bac. Bacteria inhabitants, with multiple species mix to create a microbial community. This "inhabitant-house-community" type structure regulates the social relationships within it in a certain way, maintaining the stability and ecological function of the microbial envelope. Bacteria need to colonize and accumulate on the carrier to enable them to survive and explain their ability to adhere to the material's surface.

"No man is an island," and so are bacteria. In natural environments, microorganisms colonize solid surfaces

or gas-liquid interfaces through free collisions and random selection. They secrete polysaccharides, proteins, lipid compounds, and nucleic acids to form EPS. In contrast, organisms are encapsulated in EPS to form microbial communities^[21], often referred to as biofilms. Figures 1^[22] and 2^[31] show the biofilm formation process and its composition.

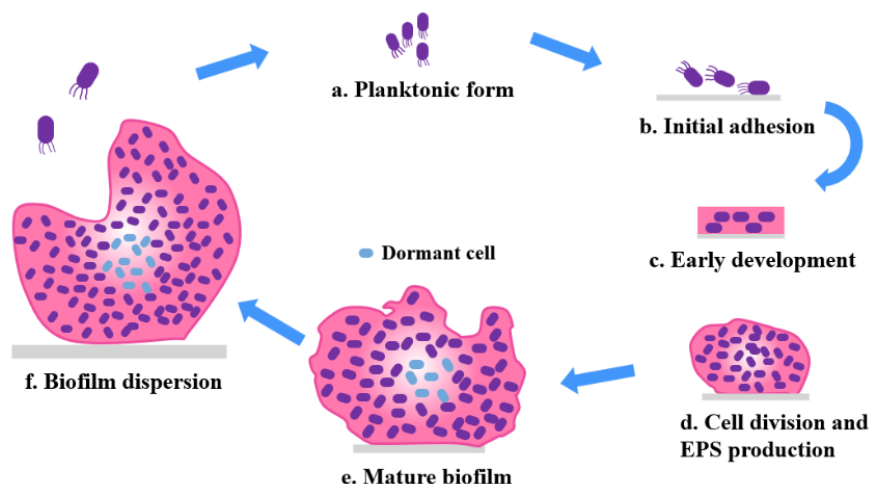


Fig. 1 Stages of biofilm formation on materials surfaces^[22]

Unlike microorganisms in their free state, biofilms are coordinated, functional, membrane-like complexes in which different species of microorganisms have diverse and extensive communication, cooperation, and competition^[23]. Biofilms have a complex structure and function, providing a relatively stable environment for the microorganisms within the membrane to survive and cope with the damage caused by adverse factors^[25]. For microorganisms, biofilm formation has three^[22,26] benefits: (1) the ability to cluster against unfavorable environments (antibiotics or host stress); (2) access to nutrients that are difficult to obtain individually; and (3) access to new genetic information through genetic drift.

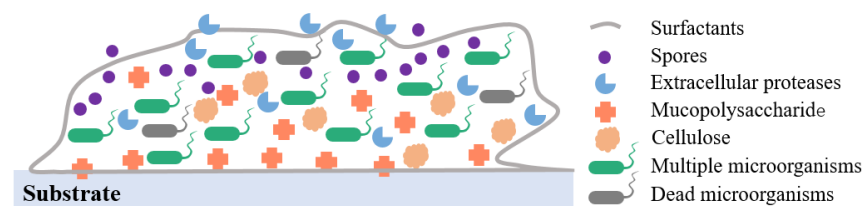


Fig. 2 Composition of biofilms^[31]

2.2 Near-interface motility behavior of bacteria

The initial aggregation of individual free bacteria and then biofilm formation is a complex and variable process influenced by several factors, such as the microbial species, the surface to which they are attached, and the surrounding environment^[12]. Straub et al.^[10] found that the interactions associated with bacterial adhesion can be classified into three types: (1) Specific interactions, (2) Non-specific physicochemical interactions, and (3) Surface mechanical sensing. This is shown in Figure 3^[10].

2.2.1 Specific interactions

In specific interactions, specific appendages of bacteria (bacterial hairs, flagella, coils) can bind to some chemicals on certain surfaces^[22]. For example, the characters of *Pseudomonas aeruginosa*, *Pseudomonas putida*, and *E. coli* appendages contain long-chain networks of polysaccharides and biopolymers that create spatial forces with the material surface^[27], which in turn facilitate their adhesion to the material surface.

2.2.2 Non-specific physicochemical interactions

In non-specific physical-chemical interactions, the adhesion of bacterial appendages and proteins occurs through non-covalent interactions with specific chemical components on the surface. The interactions, in this case, are mainly van der Waals (usually attractive), electrostatic (usually repulsive), hydrophobic, or acid-base interactions (attractive or repulsive) but are influenced by the composition of the medium, the pH of the environment, pressure, nutrients, oxygen and the nature of the surface^[12,27-30].

These interactions are related to the distance from the bacteria to the material surface. Usually, when the distance is greater than 50 nm, the van der Waals force plays a major role, and when the distance is shorter (10-20 nm), the van der Waals force and the electrostatic effect act simultaneously^[33]. When the distance is further reduced to 1.5 nm, in addition to van der Waals and electrostatic interactions, some specific interactions may also exist.^[27]

2.2.3 Surface mechanical sensing

Surface mechanosensing, on the other hand, is the ability of bacteria to sense physical contact with the substrate through mechanics^[33]. Mechanosensing triggers a signaling shift from a planktonic mode to a biofilm growth mode^[32]. Studies have shown that bacteria inhibit the rotation of pili and bacterial bodies by "sensing"^[12], providing the potential for attachment to the surface of the material and that the interaction between their sensing organs, coats, and flagella, allows for the rapid and timely production of adhesins, thus facilitating the transition from reversible to irreversible attachment^[35]. In surface mechanosensing, bacteria can actively sense when they touch a surface, and because it may involve a series of biological reactions, this effect takes longer than the first two interactions.^[12]

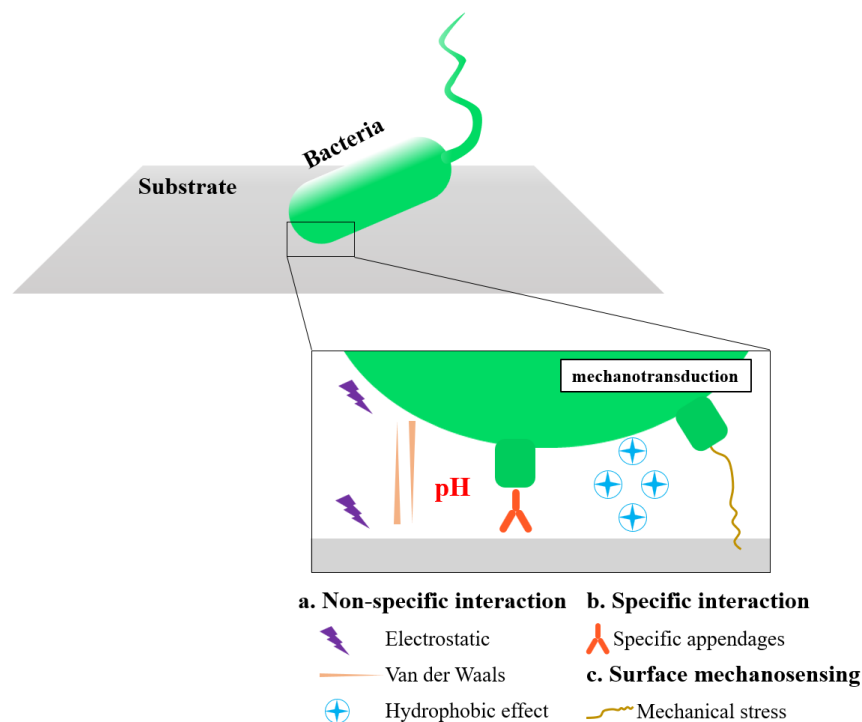


Fig. 3 Bacterial adhesion mechanisms ^[10]

3. Factors influencing adhesion

The factors influencing bacterial adhesion can be divided into three main categories: bacterial self, material, and environmental. Bacterial self factors include extracellular appendages and extracellular polymers; material characteristics include roughness, hydrophobicity, and charge; and environmental factors include flow rate, pH, and temperature. By analyzing the factors influencing bacterial adhesion to material surfaces, adequate protective measures can inhibit microbial adhesion or growth and reproduction by reducing the formation of harmful biofilms.

3.1 Bacterial factors

Cell surface properties can also influence the process of microbial membrane formation. Bacterial extracellular polymers^[34], lipopolysaccharides^[35], and flagellar hairs^[36] will have a significant impact on adhesion behavior and outcome.

3.1.1 Extracellular appendages

Henrichsen ^[37] studied the movement behavior of 40 kinds of bacteria on the surface, and summed up 6 movement modes: swimming, swarming, gliding, twitching, sliding and Darting. Bacterial motility is related to the bacteria's motility organ, the flagellum, the bacteriophage, which resembles a kind of spiral propeller that, by rotating itself, gives the cell the ability to move^[38-39]. For example, swimming is mainly due to the rotation of the flagellum ^[40], surging relies on flagella and extracellular secretions ^[41], and rubbing comes from the release and contraction of the bacteriophage^[42]. In the initial stages of bacterial attachment to the interface, flagellar motility facilitates the interaction of the bacteria with the interface, and flagellar filaments can adhere directly to the interface substrate^[27].

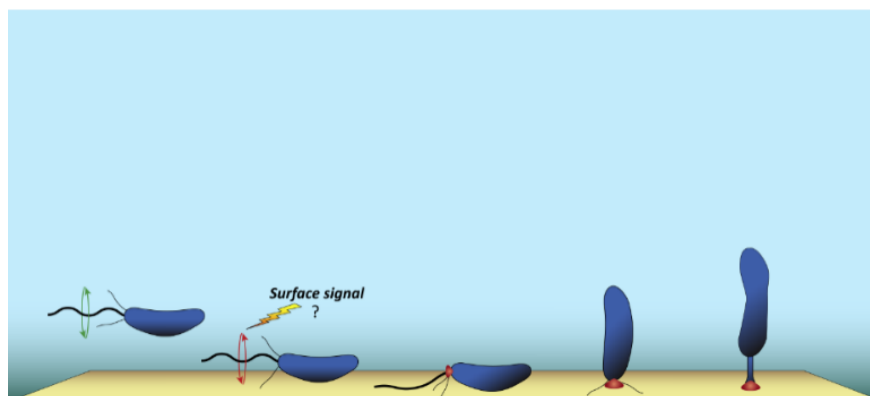


Fig. 4 Flagellum mechanical induction ^[43]

Bacteria can also swim by rotating one or more flagella, allowing them to reach speeds that exceed the length of many cell bodies per second^[44]. When the flagellum rotates counterclockwise, it generates a thrust that causes the bacteria to 'run' forward. In contrast, when the flagellum rotates clockwise to produce a 'tumble,' it inhibits the bacteria from swimming forward. In contrast, the swimming bacteria can regulate the counterclockwise/clockwise rotation of the flagellum through a complex signal ^[45], as shown in Figure 4 ^[43]. clockwise rotation^[45], as shown in Figure 4^[43].

The flagellar mechanosensing of bacteria is associated with the inhibition of flagellar rotation, with initial cell-surface 'binding' occurring through the flagellum and surface contact, causing the flagellar cycle to cease as the cell approaches the surface, resulting in the timely production of polysaccharide adhesins that cause bacteria to adhere to the surface, mediating the transition from reversible to irreversible adhesion ^[33], thereby promoting bacterial adhesion.

3.1.2 Extracellular polymers (EPS)

EPS is necessary for bacteria to form biofilms and is often used as the backbone of biofilms, playing an essential role in the stages of biofilm formation such as adhesion, proliferation, and microcolony aggregation. Once the bacteria have attached to the interface, several substances such as polysaccharide proteins secreted extracellularly make it easier for the bacteria to adhere to the interface. Then, bacterial aggregation begins to secrete more EPS, which increases the degree of adhesion and interfacial interaction between bacteria [46], gradually turning reversible into irreversible adhesion.

Ma et al. [46] showed that Psl polysaccharides promoted the adhesion and intercellular aggregation of *P. aeruginosa* PAO1 bacteria, resulting in a more dense biofilm morphological structure. EPS not only affect bacterial adhesion behavior and biofilm formation but also affects the viscoelasticity of biofilms. Firstly, Stoodley [47] and others demonstrated that biofilms are viscoelastic materials using a mathematical model to predict how they deform and fail to detach after shear stress is applied. Later, Dongen et al. [48] determined the viscoelasticity of *Streptococcus mutans* biofilms by a novel micro indentation device combined with confocal microscopy. By dragging the biofilm to break it, it was possible to find that the tensile strength of the biofilm was mainly dependent on the tensile strength of the EPS. Tsuneda et al. [49] examined cell surface characteristics such as ζ potential and hydrophobicity by a packed bed method, and when EPS was overexpressed, EPS dominated. The number of bacterial adhesions did not vary with the absolute value of ζ potential. In contrast, when EPS is expressed in small amounts, the EPS dominates, and the number of cell adhesions increases with a decrease in the absolute value of the cellular ζ potential.

Harimawan et al. [50] determined the composition of the EPS components produced during interfacial adhesion and found that the EPS layer on the surface of *Bacillus subtilis* contained more protein compounds such as γ -PGA and peptidoglycan. In contrast, the EPS layer on the surface of *Pseudomonas aeruginosa* had more polysaccharide compounds such as lipopolysaccharide, alginate, Pel, and Psl. AFM then probed the adhesion between these two bacteria and the substrate surface. The test results showed that the bonding between *Pseudomonas aeruginosa* and the interface was more significant than that between *Bacillus subtilis* and the interface, further demonstrating the presence of polysaccharides in the EPS layer enhanced the adhesion strength.

By studying EPS (with EPS as the control group and without EPS as the experimental group) on *E.coli* JM109 interfacial adhesion, Zhang^[51] found that EPS had no significant effect on bacteria-interface adhesion rate, adhesion number and other behaviors. However, after measuring the vibrational spring constant of the bacteria interface, it was found that EPS had a significant effect on the viscoelasticity of the bacteria interface, with the *E.coli* JM109 spring constant of the control group being about twice the spring constant of the *E.coli* JM109 of the experimental group, demonstrating that EPS promoted bacterial-interface adhesion and increased the bacterial-interface interaction force.

3.2 Materials factors

3.2.1 Roughness

Material surface roughness also affects bacterial adhesion, which differs between nanoscale and micron-scale roughness. There is a negative correlation between bacterial adhesion and nanoscale roughness and a positive relationship when the roughness is more significant, as shown in Figure 5 [52].

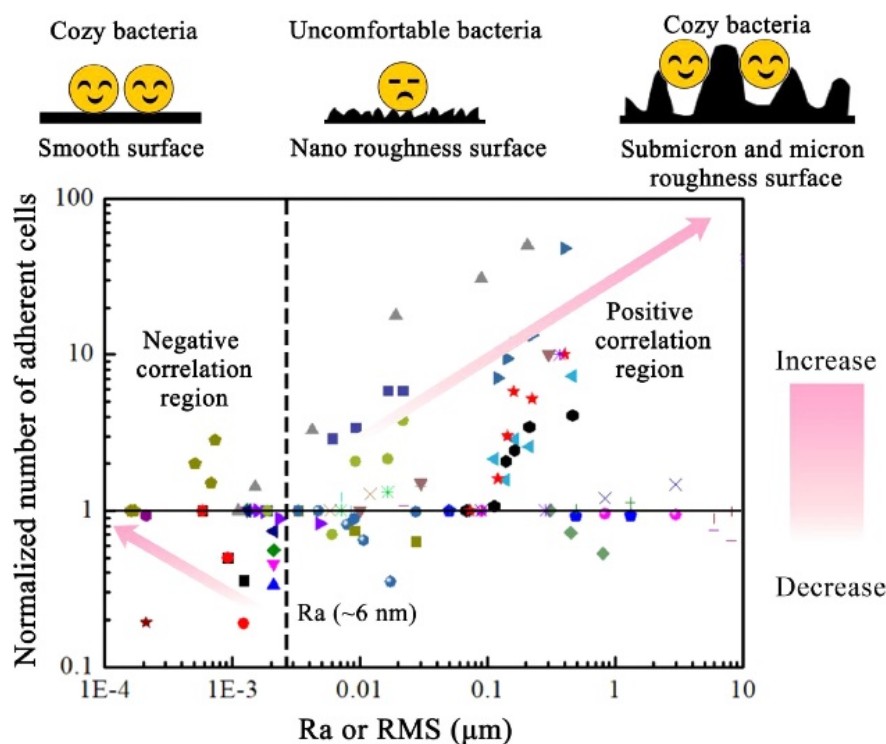


Fig. 5 Number of adherent bacteria about roughness^[52]

(1) Nano-roughness

When the roughness is minor ($Ra:0.23-6.13$ nm), smooth surfaces under static conditions are more conducive to bacterial adhesion; as the surface roughness decreases, the more bacteria adhere to the surface^[53-56]. This phenomenon is associated with cellular metabolic activity, such as an increase in bacterial size and an increase in EPS production on smooth surfaces^[54-55]. For example, the adhesion of *Staphylococcus aureus* decreases with increasing nanostructure size. This is because the macromolecules on the bacterial cell wall can only bind the top region of the material surface, and the top part decreases with increasing nanostructure size^[57], as shown in Figure 6(a).

When the roughness is relatively large ($Ra:6-30$ nm), the rough surface is more conducive to bacterial adhesion. The number of bacteria adhering to the surface increases as the surface roughness increases^[58-60]. For example, oral restorative materials with greater roughness and surface energy can increase the adhesion of *S. aureus*^[61]. A saliva coating alters this causal relation, and the layer may change the surface roughness^[12].

(2) Submicron and micron roughness

Many researchers have reported that bacterial adhesion positively correlates with the submicron or micron-scale roughness^[62-67]. The adhesion force between bacteria and surfaces with submicron scale roughness was enhanced as the roughness increased until the necessary roughness was reached^[68-70]. Bacteria attached to rougher surfaces have more obvious deformation. More considerable deformation of bacteria could increase the contact area and the adhesion force. If the roughness of the character is so high, the bacteria on the bacterial probe could only touch the protruding parts of the surface^[63, 70], as shown in Figure 6 (b). Higher roughness didn't further promote the initial adhesion in static culture conditions. At the same time, the deep valleys on the rough surface could trap bacteria and protect them from the shear force of the washing procedure, as shown in Figures 6 (b) and 6 (d).

Compared with Ra , peak density (S_{pd}) also has a significant effect on bacterial adhesion, especially at lower

roughness^[73]. Siegmund et al. combined the XDLVO theory with the surface element integration method to compare the impact of Ra and S PD on bacterial adhesion on rough titanium surfaces^[70], as shown in Figure 6. The calculation result revealed that when the average roughness was low ($Ra < 70$ nm), the interaction energy had a negative correlation with the peak density; when the average roughness was higher ($Ra > 150$ nm), the interaction energy only depended on Ra.

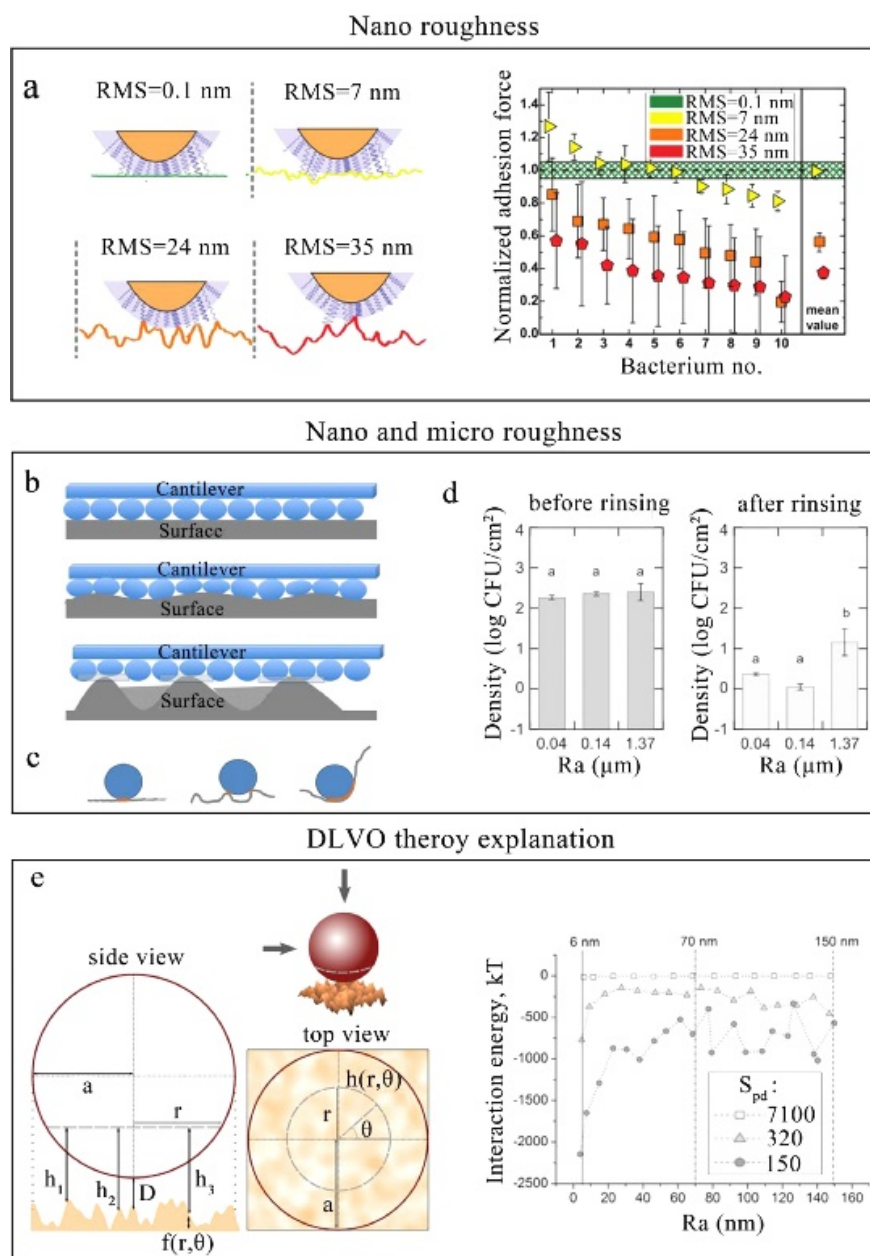


Fig. 6 Mechanism of the effect of roughness on bacterial adhesion ^[52]

3.2.2 Hydrophobicity and charge

(1) Hydrophilic and hydrophobic surfaces

Bacteria prefer to adhere to surfaces with higher hydrophobicity^[65,77-78,81-84,93]. This is mainly because of the excellent adhesion between bacteria and hydrophobic surfaces. Surface hydrophobicity can facilitate landing and bonding as bacteria approach the surface by reducing bacterial movement through collisions^[94]. During the reversible adhesion phase, *Lactobacillus Plantarum* interacts with hydrophobic end-alkyl surfaces faster and more intensely than hydrophilic end-hydroxy surfaces^[74].

However, some studies have shown that certain hydrophilic surfaces also facilitate bacterial adhesion^[79-81,85-86,95-96]. Microscopic observation revealed that fewer *Pseudomonas aeruginosa* and *Staphylococcus aureus* adhered to hydrophobic silicone surfaces than to hydrophilic surfaces^[85]. Kriegel and Ducker found that liquid films on hydrophobic surfaces evaporated more rapidly, causing adherent bacteria to leave the material's surface^[97]. Both hydrophilic and hydrophobic surfaces are suitable for the adhesion of gentamicin-resistant *Pseudomonas aeruginosa*, where the hydrophilic surface promotes the formation of microcolonies, and the hydrophobic surface encourages the production of EPS^[98].

(2) Superhydrophobic and superhydrophobic surfaces

Many studies have shown that superhydrophobic^[87-88] and superhydrophobic^[87-91,99] surfaces have the good antibacterial ability and are not conducive to bacterial adhesion. The hydrated layer on the surface of super hydrophilic TiO₂ coatings has good antimicrobial adhesion properties. However, fluids in the environment can reduce the hydrated layer's thickness and decrease its antimicrobial efficiency^[87].

On superhydrophobic surfaces, tiny air bubbles in the nanostructure can reduce the contact area of bacteria (*Pseudomonas aeruginosa*) with the material, thereby reducing their adhesion and preventing adhesion^[92,100]. However, under static incubation conditions, *S. aureus* can successfully colonize the superhydrophobic surface's three-phase interface (air, liquid and solid)^[75-76,100-101], as the superhydrophobicity of the material is sub-stable and the liquid eventually replaces these tiny air bubbles. The superhydrophobic surface can further improve the antimicrobial efficiency by binding to silver nanoparticles^[103].

(3) Electric charge

Bacteria are more likely to adhere to positively charged material surfaces because most bacteria have negatively charged cell walls^[104-105]. The effect of charge repulsion between it and bacteria on bacterial adhesion increases with the hydrophilicity of the material surface for negatively charged material surfaces^[103], so antimicrobial efficiency can be improved by modifying the positive or negative charge of the material surface. However, it was also found that many bacteria adhering to positively charged surfaces showed little growth^[106], possibly because of strong, attractive electrostatic interaction forces that inhibit the elongation and division required for bacterial growth and reproduction^[107].

3.3 Environmental factors

3.3.1 Flow rate

Water flow can promote the migration of bacteria to surfaces^[108]. Some studies have shown that increased shear force due to the fluid can increase the rate and number of bacteria adhering to the material. However, when the velocity of the fluid exceeds a critical value, the juice inhibits bacterial adhesion. It even separates bacteria that have already adhered to the aggregate, and the critical value is related to the material to which the bacteria adhere^[109]. At low flow rates, the direction of movement of adherent bacteria is random and disordered. As the flow rate increases, the orientation of the bacteria becomes closer to the streamline and aligns with the flow direction^[110].

Zhang^[111] used microfluidics to construct a micron-scale device to simulate the effect of shear force on bacteria adhering to the inner walls of micron-scale channels at different flow rates (0.5 mL/h to 1700 mL/h). The experimental results showed that: (1) the number of bacteria adhering to the surface remained constant after the shear force was increased to 200 Pa (150 m/h). The bacteria did not fall off the surface even if the shear force was increased further. The strong adhesion of the remaining bacteria on the surface may be related to their extracellular proteins and polysaccharides. (2) The number of surface-adherent

bacteria was related to the application path of the shear flow field, i.e., the number of surface-adherent bacteria under directly increasing shear stress was lower than the number of surface-adherent bacteria under the corresponding shear flow field with a gradient increase.

3.3.2 pH value

In a liquid environment, changes in pH affect the surface charge properties of bacteria through the isoelectric point theory^[112]. When the pH in the fluid domain is greater than the bacterial isoelectric point, the ionization of the carboxyl groups of amino acids on the bacterial surface makes them negatively charged; when the pH in the liquid environment is less than the bacterial isoelectric point, the ionization of the amino groups of amino acids on the bacterial surface makes them positively charged.

Sheng et al. ^[113] measured the adhesion of three bacteria (*Pseudomonas* sp, *D. desulfuricans*, and *D. Singaporeans*, with isoelectric points of 2.1, 3.5, and 2.7, respectively) to 316 stainless steel (SS316) in different pH artificial seawater (ASW) environments, as shown in Table 1.

Table 1 Force quantification of three bacteria on SS316 in ASW with different pH values ^[113]

| | pH 3 | pH 5 | pH 7 | pH 9 |
|--|-----------|-----------|-----------|-----------|
| Adhesion force of <i>Pseudomonas</i> sp. (nN) | 2.8±0.4 | 2.1±0.6 | 1.9±0.4 | 2.7±0.5 |
| Adhesion force of <i>D. desulfuricans</i> (nN) | 2.4±0.2 | 1.7±0.2 | 0.5±0.1 | 0.7±0.1 |
| Adhesion force of <i>D. Singaporeans</i> (nN) | 3.3±0.4 | 3.0±0.2 | 0.8±0.3 | 2.3±0.5 |
| Zeta potential of SS316 (mV) | 1827±36.4 | 1434±11.2 | 1350±25.6 | 1328±39.8 |

Table 1 shows that the adhesion of the three bacteria to SS316 is most excellent at pH 3, decreases when pH increases to 5 and 7 and is least at pH 7. The increase in adhesion at pH 9 is probably due to the ionization of the functional groups (carboxyl and amino groups) on the surface of the bacteria as pH changes.

As the pH rises from 3 to 7, the ionization of the carboxyl groups becomes weaker and more robust. The electrostatic gravitational force between the bacteria and the metal surface gradually increases. Still, at pH 3, the zeta potential of the bacteria approaches 0. The thin double electric layer (EDL) at the solid-liquid interface plays a decisive role. Hence, the bacteria reach the SS316 surface with the lowest adhesion barrier and thus the highest adhesion force. As the pH rises to 9, the concentration of negatively charged COO^- in the liquid environment is more elevated and . It combinestrostatically with the presence of Fe^{2+} on the SS316 surface to produce more excellent adhesion.

3.3.3 Temperature

At optimum temperatures, bacteria can increase their uptake of nutrients, allowing rapid biofilm formation ^[114]. Nutrient metabolism depends on and is directly influenced by the presence of enzymes. Temperature is related to the reaction rate of enzymes, making temperature one of the factors determining the metabolic efficiency of cells. The optimal temperature will lead to healthy growth of bacterial populations, and vice versa will reduce the efficiency of bacterial growth.

In addition to the effect on enzymes, environmental temperature also affects the physical properties of compounds within and around cells. By studying the effect of temperature on cell attachment in the stationary phase, Fletcher ^[115] found that a decrease in temperature promoted a reduction in the adhesion properties of *Pseudomonas Maritima*, which may be related to the decline in bacterial surface polymers, surface area, at low temperatures.

Herald and Zottola ^[116] found that the presence of bacterial surface appendages was closely related to temperature. At 35 °C, the cells had one flagellum; at 21 °C, they had two to three flagella; at ten °C multiple flagella appeared. This suggests that the initial interaction between the bacteria and the substrate may increase as the temperature decreases, thus increasing bacterial adhesion.

4. Adhesion test method

Several techniques can be applied to measure cell adhesion force^[117]. It can be divided into two main categories: population cell and single-cell methods, as shown in Figure 7. Many of them, including the simple washing assay, the spinning disk technique, and flow chambers, are based on the hydrodynamic shear flow removing cells from the surface. The adhesion force can be calculated from the applied flow rate, and thus, the adhesion force of the cells can be measured. However, these techniques do not enable single-cell targeting, and cell shape strongly impacts the shear force, making it difficult to calculate the exact adhesion force. Furthermore, only weakly adhered cells can be probed due to the technically limited shear stress magnitude.

In order to directly probe the adhesion of single cells, an AFM probe or micropipette can be used as an option.^[118-120] Single-cell adhesion assay techniques can be further classified according to how they work. The micropipette aspiration uses a glass micropipette to suck cells from the surface and calculates adhesion forces by hydrodynamic simulation. AFM is combined with modified probes or nanofluidic channels to study cell adhesion. Fluorescence resonance energy transfer (FRET) sensors can also be used to detect transgenic cell protein fluorescence signals to characterize the mechanical tension of cells and to measure the traction force generated by adherent cells in the substrate.

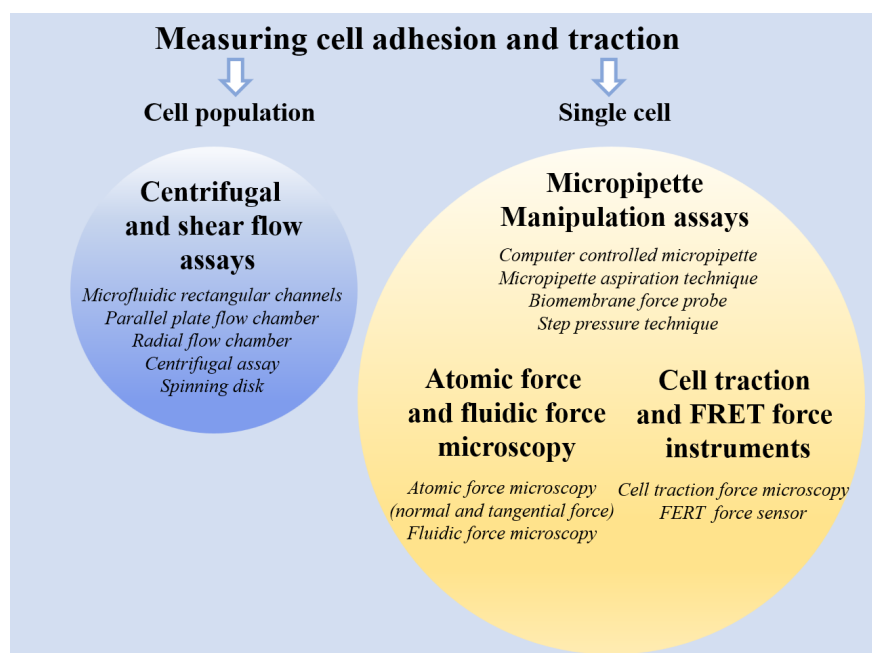


Fig. 7 Classification of cell adhesion measurement techniques^[117]

AFM is now commonly used to measure the adhesion of bacteria to surfaces. The AFM developed by Binnig et al.^[121] uses force-sensitive cantilevers to probe the interaction forces between the needle tip and the character, thereby obtaining a microscopic picture of the sample surface on the nanometre scale. Single-cell force spectroscopy (SCFS) is a bacterial probe prepared by immobilizing a single bacterium on a micro-cantilever, which can be used to measure the interaction forces between bacteria and various surfaces and between bacteria and bacteria as shown in Figure 8^[122].

First, individual cells are immobilized at the free end of a non-tilted cantilever beam^[123], and the process of functionalizing the probe is achieved by attaching individual cells to the AFM cantilever with agglutinin, ensuring that the surface of the cell is not modified. The functionalized examination then comes into contact with the character or another cell and the cantilever is pulled back at a constant rate to separate the cell from its contact end, and the deflection of the cantilever is detected using a laser beam focused on the top

of the cantilever and reflected a quadrant photodiode^[124]. The cantilever beam deflection is proportional to the force acting between the surface and the cell, resulting in a force-distance curve^[122]. AFM can measure the adhesion of cells attached to the cantilever to the substrate surface and the adhesion of cells immobilized on the substrate to the cantilever^[125].

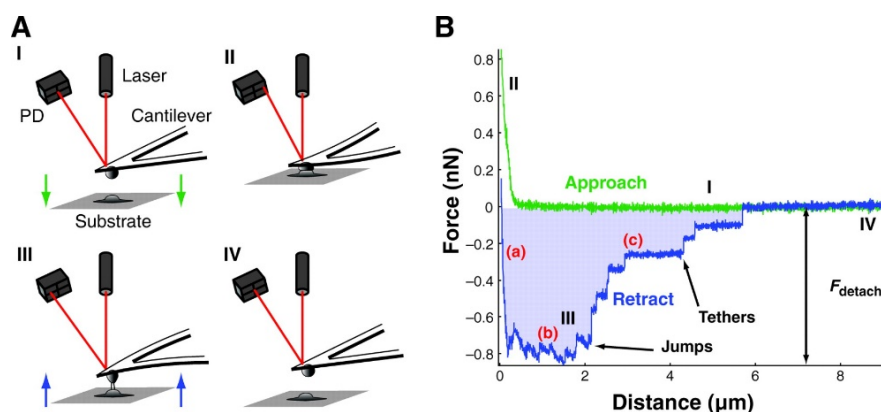


Fig. 8 Single-cell force spectroscopy^[122]

The AFM can measure the adhesion force of individual intact living cells with high spatial and energy resolution, pico-newton-scale force sensitivity, and nanometre-scale localization accuracy. AFM has unique features: (1) it can operate in solution and observe biological structures under in situ conditions^[129]. (2) it can observe individual proteins at a resolution greater than 1 nm, allowing direct observation of structural changes in individual biomolecules^[128].

AFM also has limitations, such as the time-consuming and expensive measurement of bacterial adhesion using single-cell force spectroscopy. Only one cell can be characterized at a time; each cell requires a separate cantilever and must be calibrated and functionalized^[122,125,127], falling short of high throughput measurements^[128]. Using lectins to put fixed cells on cantilever beams is time-consuming and tends to alter the original physiological properties of the cells^[126]. To obtain reliable data, a large number of force-distance curves need to be measured.

5. Conclusion and perspective

Research work on harmful bacterial adhesion and its biofilm formation in the future will remain a top priority in the fields of biomedicine, agriculture, food industry, drinking water and marine environment. However, as researchers continue to gain a deeper understanding of the two sides of bacterial adhesion and its biofilm effect, remarkable achievements have been made in plant protection, microbial remediation, wastewater treatment, and microbial corrosion control. This paper puts forward the following suggestions for the future development of bacterial adhesion research, in order to attract relevant scholars to pay more attention and research on bacterial adhesion and biofilm formation.

- (1) Efficient control of harmful bacterial adhesion, deepening research on factors affecting bacterial adhesion and providing theoretical guidance for the construction of antibacterial surfaces with excellent performance.
- (2) In-depth research on the regulatory mechanism of bacterial adhesion, biofilm formation, and diffusion, especially the study related to beneficial bacterial adhesion; explore the application scheme of bacterial biofilm and its practical application in engineering.
- (3) The phenomenon of bacterial adhesion is a complex disciplinary problem involving biology, materials science, environmental science, etc. It involves in-depth cross-analysis and application of theoretical knowledge of various disciplines. It is necessary for scholars to have a sufficient and comprehensive knowledge system in order to systematically, comprehensively and accurately grasp the bacterial adhesion surface and

its mechanism of action. It is also necessary for scholars in related fields to cooperate and communicate with each other.

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