

Surface Thermodynamics of Bacterial Adhesion

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The adhesion of five strains of bacteria, i.e., *Staphylococcus aureus* (strain 049), *Staphylococcus epidermidis* (strain 047), *Escherichia coli* (strains 055 and 2627), and *Listeria monocytogenes*, to various polymeric surfaces was studied. The design of the experimental protocol was dictated by thermodynamic considerations. From the thermodynamic model for the adhesion of small particles from a suspension onto a solid substratum, it follows that the extent of adhesion is determined by the surface properties of all three phases involved, i.e., the surface tensions of the adhering particles, of the substrate, and of the suspending liquid medium. In essence, adhesion is more extensive to hydrophilic substrata (i.e., substrata of relatively high surface tension) than to hydrophobic substrata, when the surface tension of the bacteria is larger than that of the suspending medium. When the surface tension of the suspending liquid is larger than that of the bacteria, the opposite pattern of behavior prevails. Suspensions of bacteria at a concentration of 10^8 microorganisms per ml were brought into contact with several polymeric surfaces (Teflon, polyethylene, polystyrene, and acetal and sulfonated polystyrene) for 30 min at 20°C. After rinsing, the number of bacteria adhering per unit surface area was determined by image analysis. The surface tension of the suspending medium, Hanks balanced salt solution, was modified through the addition of various amounts of dimethyl sulfoxide. It was found that the number of bacteria adhering per unit surface area correlates well with the thermodynamic predictions and that these data may be used to determine the surface tension of the different bacterial species. The surface tensions of the bacteria obtained in this fashion are in excellent agreement with those obtained by other methods.

Bacterial adhesion to a surface is known to play an important role in a wide variety of situations, e.g., infection of various tissues (21), dental decay (16), ship fouling (9), fermentation (5), and wastewater and sewage treatment (6). However, the fundamental mechanisms governing bacterial adhesion are poorly understood and have not been well defined. Most work to date on microbial adhesion has dealt with the influence of substrata surface properties on the extent of the relative adhesion (7), growth of the adhering microbes, and their subsequent behavior (8). A brief survey of the abundant literature from various diverse disciplines such as experimental pathology, the evaluation of synthetic vascular implant materials, etc., suggests that a qualitative relationship exists between the surface properties of the various synthetic (usually polymeric) materials and the extent of the biological response (e.g., cell adhesion, phagocytic ingestion, or fibrous encapsulation) they evoke.

In view of the pervasive nature of bacterial adhesion, the present study was undertaken in an attempt to define those parameters which determine the extent of the initial interaction of bacterial adhesion to polymer surfaces. Such details are required if one is to understand, control, and modify such microorganism-substratum interactions in various technological areas such as preventing unwanted biofouling or improving colonization of cells onto synthetic surfaces.

Theoretical considerations. Our approach to this problem is based on surface thermodynamics. This implies that a properly identified thermodynamic potential, i.e., the free energy, will be minimized at equilibrium. Thus, the process under consideration, bacterial adhesion, will be favored if the process itself causes the thermodynamic function to decrease. The process will not be favored if it causes the free energy function to increase. For systems in which the

effect of electric charges as well as specific biochemical interactions (e.g., receptor-ligand) may be neglected, the change in the free energy function (ΔF^{adh}) is, per unit surface area:

$$\Delta F^{\text{adh}} = \gamma_{BS} - \gamma_{BL} - \gamma_{SL} \quad (1)$$

where F^{adh} is the free energy of adhesion, γ_{BS} is the bacterium-substratum interfacial tension, γ_{BL} is the bacterium-liquid interfacial tension, and γ_{SL} is the substratum-liquid interfacial tension. Although equation 1 by itself constitutes nothing more than a simple free energy balance, only in recent years has it become possible to obtain experimental data for the various interfacial tensions involving solid surfaces. Briefly, this is achieved through the use of Young's equation:

$$\gamma_{SV} - \gamma_{SL} = \gamma_{LV} \cos \theta \quad (2)$$

where γ_{SV} , γ_{SL} , and γ_{LV} are, respectively, the interfacial tension between a solid substratum S and the vapor phase V , between S and the liquid L , and between L and V ; θ represents the contact angle of the liquid on the solid (14). Of the four quantities in equation 2, only the liquid surface tension (γ_{LV}) and θ are readily determined experimentally; determination of a further relation between these quantities is required. It has been shown from thermodynamic considerations that an equation of state relation of the form:

$$\gamma_{SL} = f(\gamma_{SV}, \gamma_{LV}) \quad (3)$$

must exist (20). Using experimental contact angle data and liquid-vapor interfacial tensions, equation 3 has been formulated explicitly (14) as follows:

$$\gamma_{SL} = \frac{\left(\sqrt{\gamma_{SV}} - \sqrt{\gamma_{LV}}\right)^2}{1 - 0.015 \sqrt{\gamma_{SV} \cdot \gamma_{LV}}} \quad (4)$$

In conjunction with Young's equation, this relation yields:

$$\cos \theta = \frac{(0.015 \gamma_{SV} - 2.00) \cdot \sqrt{\gamma_{SV} \cdot \gamma_{LV}} + \gamma_{LV}}{\gamma_{LV} \left(0.015 \sqrt{\gamma_{SV} \cdot \gamma_{LV}} - 1\right)} \quad (5)$$

With the aid of equation 5 the unknown surface tension of the substratum, γ_{SV} , may be determined from the easily measurable quanti-

ties γ_{LV} and θ . If equation 4 is considered as a generic equation to calculate any interfacial tension γ_{12} from (given or predetermined) interfacial tensions γ_{13} and γ_{23} , where the subscripts 1, 2, and 3 refer to different phases, all required interfacial tensions in equation 1 may be computed, permitting explicit thermodynamic predictions of the relative extent of bacterial adhesion to various substrata.

Equations 4 and 5 have, as they stand, certain purely mathematical limitations which can, however, be circumvented (11, 14). Computer programs (15) as well as tables (11) are available which avoid such difficulties.

The purpose of the present paper is to study the effect of the surface tension of substrata (γ_{SV}) and of the suspending liquid medium (γ_{LV}) on the relative extent of adhesion of five strains of bacteria to a wide range of polymer surfaces. A theoretical calculation of the free energy change (ΔF^{adh}) for the attachment of bacteria from suspension to various substrata as a function of γ_{SV} is illustrated in Fig. 1. The input data required for the development of such a plot are the surface tensions of the three interacting species, i.e., the surface tensions of the bacteria (γ_{BV}), the polymer substrata (γ_{SV}), and the suspending liquid medium (γ_{LV}). Such theoretical calculations lead to a distinction between two situations. For

$$\gamma_{LV} < \gamma_{BV} \quad (6)$$

where γ_{BV} is the interfacial tension between the bacteria and vapor, ΔF^{adh} decreases with increasing γ_{SV} , predicting increasing bacterial adhesion with increasing surface tension (γ_{SV}) of the substrate over a comparatively wide range of γ_{SV} values. On the other hand, when

$$\gamma_{LV} > \gamma_{BV} \quad (7)$$

the opposite pattern of behavior occurs. A typical plot of this type is presented in Fig. 1, where the predicted adhesion of a single species of bacteria to a range of polymer surfaces, out of a series of liquid surface tensions, is depicted. For the limiting case of the equality

$$\gamma_{LV} = \gamma_{BV} \quad (8)$$

ΔF^{adh} becomes equal to zero independently of the value of γ_{SV} . The latter fact can also be seen directly from the properties of the equation of state for interfacial tensions (14), since for the case of equation 8, it follows immediately that $\gamma_{BL} = 0$ and $\gamma_{BS} = \gamma_{SL}$ (cf. equation 1). This limiting condition implies that bacterial adhesion, under these circumstances, does not depend on the surface tension of the substratum and, in principle, should be zero if no other effects, such as electrostatic interactions, come into play (2).

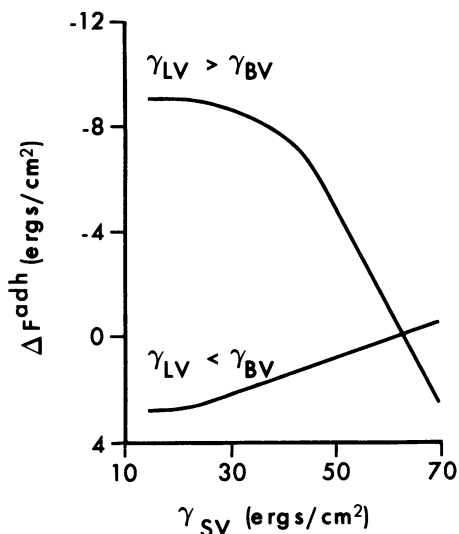


FIG. 1. Free energy of adhesion of a single bacterial species as a function of substrate surface tension. The bacterium considered is *E. coli* 2627 with a surface tension $\gamma_{BV} = 67.8$ ergs/cm². $\gamma_{LV} > \gamma_{BV}$; $\gamma_{LV} = 72.8$ ergs/cm². $\gamma_{LV} < \gamma_{BV}$; $\gamma_{LV} = 64.0$ ergs/cm².

MATERIALS AND METHODS

Bacterial adhesion. Bacterial adhesion experiments were performed with the substrate materials listed in Table 1, with surface tensions ranging from 16 to 67 ergs/cm². Preparation of the surfaces was performed as described previously and as indicated in Table 1 (2). The suspending liquid medium in these experiments was Hanks balanced salt solution, with different concentrations of dimethyl sulfoxide (DMSO), up to a maximum of 15% (vol/vol), resulting in a range of liquid surface tensions from 72.8 to 64.0 ergs/cm² (Table 2) (1 erg/cm² = 1 mJ/cm²). The pH was maintained at pH 7.1 through the addition of 0.1 M NaOH.

Preparation of bacterial suspension. *Staphylococcus aureus* (strain 049), *Staphylococcus epidermidis* (strain 047), and *Escherichia coli* (strains 055 and 2627) were lawned for 24 h at 37°C on nutrient agar (Difco Laboratories, Detroit, Mich.). *Listeria monocyto-*

genes was grown for 48 h at 37°C in tryptic soy broth. The bacteria were removed from the respective growth media, washed three times with Hanks balanced salt solution by repeated centrifugation at 475 × g for 25 min, and finally suspended in the appropriate liquid (Table 2) as determined by the experimental protocol. The bacterial concentration, determined with triplicate counts on a Neubauer counting chamber, was adjusted to yield 10⁸ bacteria per ml. (To overcome any possible problems due to bacterial clumping, the suspensions were vortexed immediately before use and counting.)

Surface tension determinations. Determination of the surface tension (γ_{SV}) of the solid substrata listed in Table 1 was performed by means of contact angle measurements via the equation of state approach (14), as described above.

Determination of the surface tension of the various suspending liquid media was performed by means of the Wilhelmy plate method (13).

The surface tensions of the various bacterial species (γ_{BV}) were determined by means of contact angle measurements on layers of the cellular material (19) via the equation of state approach (14). To this end, 10 ml of the washed bacterial suspension at a concentration of 10⁸ bacteria per ml was centrifuged at 475 × g for 25 min. The resulting pellet was resuspended in 1 ml of Hanks balanced salt solution. A 0.25-ml portion of this suspension was then evenly spread over a 1-cm² area of 1% (wt/vol) agar containing 10% (vol/vol) glycerol. A 5- μ l amount of 0.15 M NaCl, pH 7.1, was used to determine the advancing contact angle of the various species of bacteria by following the effect of the evaporation of excess water from the bacterial layer on the contact angle (19).

Adhesion protocol. Adhesion tests of the bacteria to the various substrate materials were performed as described previously for the static adhesion test with platelets (15), granulocytes (2, 12), and proteins (18). Briefly, 1 ml of the bacterial suspension containing 10⁸ bacteria, in the appropriate test medium, was placed on the surfaces and was retained in wells formed from 0.25% (wt/vol) agarose (Calbiochem, La Jolla, Calif.).

The bacteria were then incubated at 21°C for 30 min, after which the surfaces were rinsed with Hanks balanced salt solution to remove nonadherent bacteria. Thereafter, the substrates were air dried, and the cells adhering to the various surfaces were counted with an automatic image analysis system (Omnicon

TABLE 1. Solid substrates used in bacterial adhesion experiments

Material	Source	Prepn	Contact angle with water ($^{\circ}$ H ₂ O [°])	Surface tension γ_{SV} (ergs/cm ²)
Fluorinated ethylene-propylene copolymer	Commercial Plastics, Toronto, Canada	Heat press	110 ± 3	16.4
Polystyrene	Central Research Lab, Dow Chemical Co.	Used as received	95 ± 2	25.6
Low-density polyethylene	Commercial Plastics, Toronto, Canada	Heat press	84 ± 4	32.5
Acetal resin	Commercial Plastics, Toronto, Canada	Heat press	64 ± 1	44.6
Sulfonated polystyrene	Central Research Lab, Dow Chemical Co.	Used as received	24 ± 3	66.7

TABLE 2. Surface tension of suspending medium at 21°C

Medium	Concn of DMSO (% , vol/vol) ^a	Surface tension γ_{LV} (ergs/cm ²)
HBSS ^b		72.8
HBSS-DMSO 3 ^c	3	70.8
HBSS-DMSO 7.5	7.5	69.0
HBSS-DMSO 10	10	67.5
HBSS-DMSO 15	15	64.0

^a DMSO was obtained from Fisher Scientific Co., Pittsburgh, Pa.

^b Hanks balanced salt solution (HBSS) is composed of the following, in milligrams per liter: anhydrous CaCl₂, 140.0; KCl, 400; KH₂PO₄, 60.0; MgCl₂ · 6H₂O, 100.0; MgSO₄ · 7H₂O, 100.0; NaCl, 8,000.0; NaHCO₃, 350.0; Na₂HPO₄ · 2H₂O, 60.0; glucose, 1,000.0; μ = 0.15, pH 7.26.

^c Approximate concentrations (percent, volume/volume) of DMSO. Since this material is quite hydrophilic, the apparent concentrations fluctuate considerably as a function of the time the bottle (or vial) has been opened; the important value is the surface tension (γ_{LV}), measured just before use (via the Wilhelmy method).

3000; Bausch & Lomb, Rochester, N.Y.) and expressed as the number of bacteria per unit area of test surface.

RESULTS AND DISCUSSION

To use the predictive model (Fig. 1), it is necessary to know the surface tensions (γ_{LV}) of the suspending liquids, as well as the surface tensions (γ_{BV}) of the bacteria and that (γ_{SV}) of the various substrata.

Surface tensions γ_{BV} and γ_{SV} were obtained from contact angle measurements as already described. The γ_{SV} values are given in Table 1, together with the mode of preparation. The liquid surface tensions, γ_{LV} , of the buffer and buffer-DMSO mixtures are summarized in Table 2.

The contact angles measured on the various bacteria are plotted in Fig. 2. The contact angles of the plateaux represent Young contact angles, i.e., angles which are thermodynamically characteristic for the surface tension of the substrate (in this case bacteria) and not influenced by, e.g., surface roughness (14). These contact angles (Table 3) are usually stable for 20 to 50 min. From the surface tension $\gamma_{LV} = 72.8$ ergs/cm² for saline at 21°C, the surface tensions of the bacteria (γ_{BV}) were calculated as explained above (see summary in Table 3).

As an illustration of the influence of surface tension of the different bacterial species, the extent of adhesion of the five strains suspended in the standard buffer ($\gamma_{LV} = 72.8$ ergs/cm²) is depicted in Fig. 3. The extent of adhesion as well as the slope of these curves decrease with in-

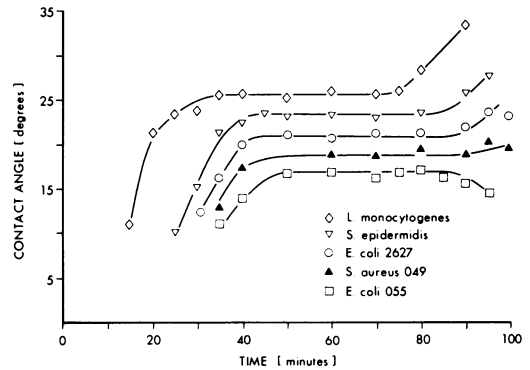


FIG. 2. Contact angles of saline on layers of bacteria as a function of water evaporation from the wet biological substrate, measured in terms of time. Each symbol represents the average of 10 individual contact angle readings on each of four different drops, at approximately the same time, on the same substrate.

creasing hydrophilicity of the bacteria (see Table 3). This difference in the slopes of these curves is significant, as will be shown below.

The results of the bacterial adhesion experiments from the various DMSO-water mixtures are given in Fig. 4. The theoretical predictions inherent in Fig. 1 and their implications are substantiated experimentally. At the lowest DMSO concentration, corresponding to the highest surface tension γ_{LV} of the suspending medium, bacterial adhesion decreases with increasing γ_{SV} of the substratum. As the DMSO concentration is increased and the surface tension γ_{LV} is correspondingly lowered, the change in the degree of bacterial adhesion with increasing γ_{SV} becomes less pronounced. At certain intermediate γ_{LV} values, specific for each bacterial species, adhesion becomes independent of γ_{SV} and finally, at yet lower values of the surface tension γ_{LV} , adhesion increases with increasing γ_{SV} .

Aside from the intrinsic interest of these data, there are two further points to be made. First, the simple thermodynamic model underlying equation 1, together with the equation of state approach for interfacial tensions (14), describes

TABLE 3. Contact angles with saline and surface tensions of bacteria at 21°C^a

Specimen	Contact angles (°)	Surface tension (ergs/cm ²)
<i>E. coli</i> 055	16.7 ± 1.0	69.7 ± 0.4
<i>S. aureus</i> 049	18.5 ± 1.2	69.1 ± 0.6
<i>E. coli</i> 2627	21.2 ± 0.7	67.9 ± 0.3
<i>S. epidermidis</i>	23.4 ± 0.5	67.1 ± 0.3
<i>L. monocytogenes</i>	26.1 ± 1.2	66.3 ± 0.6

^a The errors are 95% confidence limits.

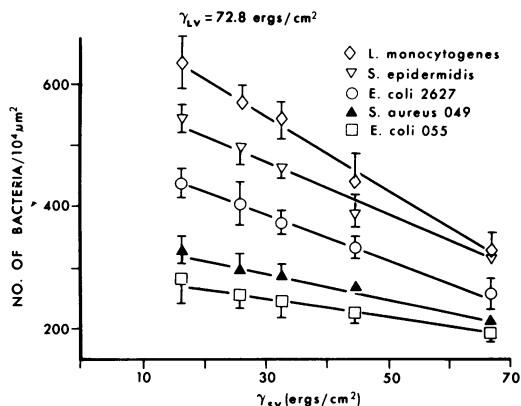


FIG. 3. Adhesion of the five bacteria to the various polymer substrates at a single liquid surface tension ($\gamma_{LV} = 72.8$ ergs/cm²). Error limits are 95% confidence limits. (For graphical reasons error limits are given only for some cases; the errors are similar in all cases.)

the qualitative features of bacterial adhesion well. Second, the data of Fig. 4 lend strong support to the method of contact angle measurement on layers of microorganisms (19). The thermodynamic model predicts that in the case of $\gamma_{LV} = \gamma_{BV}$ (equation 8), ΔF^{adh} should be independent of γ_{SV} , a situation that is indeed contained in the curves of Fig. 4. To investigate this concept further, the slopes of the straight lines in Fig. 4 were plotted versus γ_{LV} in Fig. 5, by means of a second-order polynomial computer fit. For each of the bacteria investigated it is inferred that the slope becomes equal to zero at a value of γ_{LV} characteristic for each bacterial species. This γ_{LV} value, according to the thermodynamic model, is equal to the surface tension of the adhering microorganism. For example, consideration of Fig. 5 reveals that for *L. monocytogenes* the adhesion slope becomes equal to zero when $\gamma_{LV} = 65.6$ ergs/cm², implying that the surface tension of this bacterial species is also equal to 65.6 ergs/cm². This is in excellent agreement with the value of $\gamma_{BV} = 65.8$ ergs/cm² obtained from the contact angle $\theta_{saline} = 26.1^\circ$, via the equation of state approach (Table 3), and also with the values of $\gamma_{BV} = 66.1$ ergs/cm² and 66.3 ergs/cm² obtained from phagocytic ingestion studies by human granulocytes (4) and porcine platelets (1), respectively. The experimental results obtained with the present technique, i.e., the intercepts in Fig. 5 for the five bacterial strains, are summarized in Table 4. Also given, for comparison, are the surface tension data for these bacteria obtained via other methods. In all cases the discrepancy between the various methods is <1 erg/cm².

Thus, the simple thermodynamic model proposed in equation 1, and illustrated in Fig. 1, can

be used to describe qualitatively bacterial adhesion to a range of polymer surfaces under conditions of varying γ_{LV} . However, there are certain complications which become apparent when we plot the predictions of the thermodynamic model as well as the experimental results versus the liquid surface tension γ_{LV} rather than the surface tension γ_{SV} of the substrata (Fig. 6).

From the data in Tables 1, 2, and 3, the various values of the relevant interfacial ten-

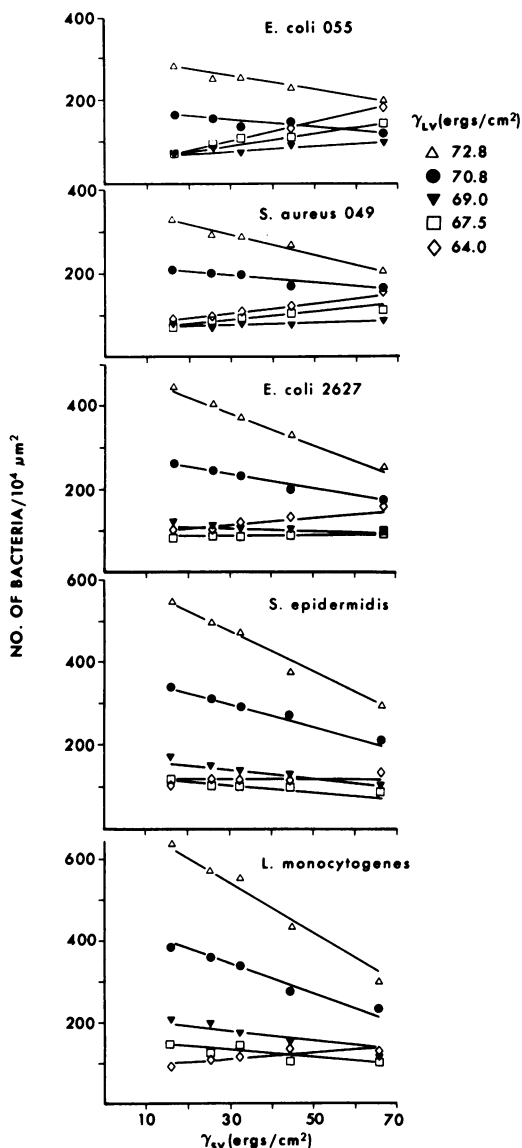


FIG. 4. Bacterial adhesion as a function of substrate surface tension γ_{SV} for various DMSO concentrations. Errors are similar in all cases to those indicated in Fig. 3.

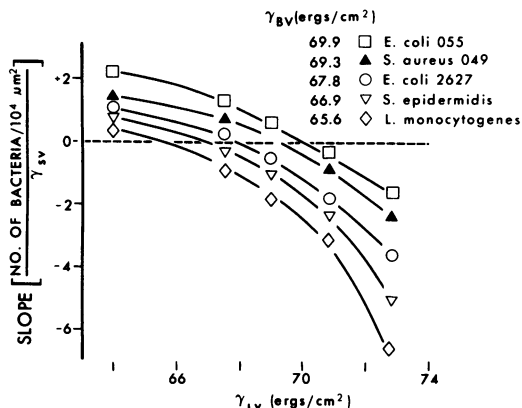


FIG. 5. Slopes of the straight lines of Fig. 4 versus γ_{LV} . The slope is zero for $\gamma_{LV} = \gamma_{BV}$.

sions γ_{BS} (bacterium-substratum), γ_{BL} (bacterium-liquid), and γ_{SL} (substratum-liquid), and hence ΔF^{adh} (see equation 1), were calculated and plotted in Fig. 6, on the right-hand side. These curves represent theoretical predictions, on the basis of the data in Tables 1, 2, and 3, to be compared with the actual (experimental) extent of bacterial adhesion represented on the left-hand side of Fig. 6. Figure 6a illustrates bacterial adhesion to a copolymer of fluorinated ethylene-propylene, the most hydrophobic surface used. Figure 6e illustrates bacterial adhesion as a function of γ_{LV} to sulfonated polystyrene, the most hydrophilic surface used in this study.

In the case of sulfonated polystyrene (Fig. 6e), the negative free energy of adhesion, as plotted on the right-hand side, shows a minimum at a certain value of γ_{LV} that is intermediate between γ_{BV} and γ_{SV} for each of the five bacteria, and it is equal to zero (with a common intercept) for all bacteria at $\gamma_{LV} = \gamma_{SV}$ (i.e., 66.7 ergs/cm²). It is to be noted that the general appearance of the curves on the right-hand side as well as these two main features are fairly closely reflected in the experimental curves for bacterial adhesion to sulfonated polystyrene (Fig. 6e, left-hand side). It is pertinent to point out that the extent of adhesion over the range of γ_{LV} values used is such that for γ_{LV} values which are >66.7 ergs/cm² (i.e., the surface tension of sulfonated polystyrene) adhesion increases with increasing bacterial hydrophobicity. However, when $\gamma_{LV} < 66.7$ ergs/cm², it is the more hydrophilic bacteria which adhere most extensively. This reversal in adhesion pattern is in accord with the thermodynamic predictions. By comparison, however, the agreement between theory (Fig. 6a, right) and experiment (Fig. 6a, left) is not as close when one examines the characteristics of bacte-

rial adhesion to a low-energy substratum, e.g., fluorinated ethylene-propylene, as a function of γ_{LV} (Fig. 6a). Theoretically, it would be expected that bacterial adhesion to the low-energy substrates would decrease linearly with decreasing γ_{LV} and, over the range of γ_{LV} values investigated, adhesion to all of the polymer surfaces should be most extensive for the more hydrophobic bacteria (Fig. 6, right). When $\Delta F^{adh} > 0$ (a situation that occurs when $\gamma_{SV} < \gamma_{LV} < \gamma_{BV}$), it is expected that there should be no adhesion to the polymer surfaces (cf. Fig. 1). Experimentally, however, it was observed that adhesion initially decreases in a linear fashion with decreasing γ_{LV} (in accord with the thermodynamic predictions) and then flattens out and becomes independent of γ_{LV} (cf. Fig. 6, left). Whereas this leveling effect is what would be expected, it was not anticipated that there would be a significant level of bacterial adhesion under these conditions, i.e., when $\Delta F^{adh} > 0$. At this time we have no definite explanation for this behavior. The deviation from linearity appears to occur only in those situations where the surface tension of the suspending liquid γ_{LV} is less than the surface tension of the bacteria, γ_{BV} , i.e., when $\gamma_{LV} < \gamma_{BV}$.

A similar situation was reported previously for the adhesion of granulocytes to polymer substrata (2, 12), where adhesion took place in spite of the fact that the free energy of adhesion was positive or zero. Such behavior was found to be the result of electrostatic interactions between the polymeric substrata and the cells, mediated by plurivalent cationic bridging (3). When the ionic strength of the liquid was lowered and a chelating agent was incorporated into the suspending medium, cell adhesion could indeed be reduced to virtually zero, when the free energy of adhesion was positive (3). It is possible and indeed likely (17) that a similar mechanism plays a role in determining the over-

TABLE 4. Comparison of surface tension of various bacteria obtained via different methods

Bacteria	Surface tension (ergs/cm ²) obtained via indicated strategy			Adhesion ^b
	Contact angle via equation of state ^a	Phagocytic ingestion		
		Granulocytes ^a	Platelets ^a	
<i>E. coli</i> 055	69.7	69.6	69.3	69.9
<i>S. aureus</i> 049	69.1	68.7	68.9	69.3
<i>E. coli</i> 2627	67.8	ND ^c	ND	67.8
<i>S. epidermidis</i>	67.1	66.9	67.3	66.9
<i>L. monocytogenes</i>	66.3	66.1	65.8	65.6

^a See references 1 to 4 and 17.

^b This work.

^c ND, Not done.

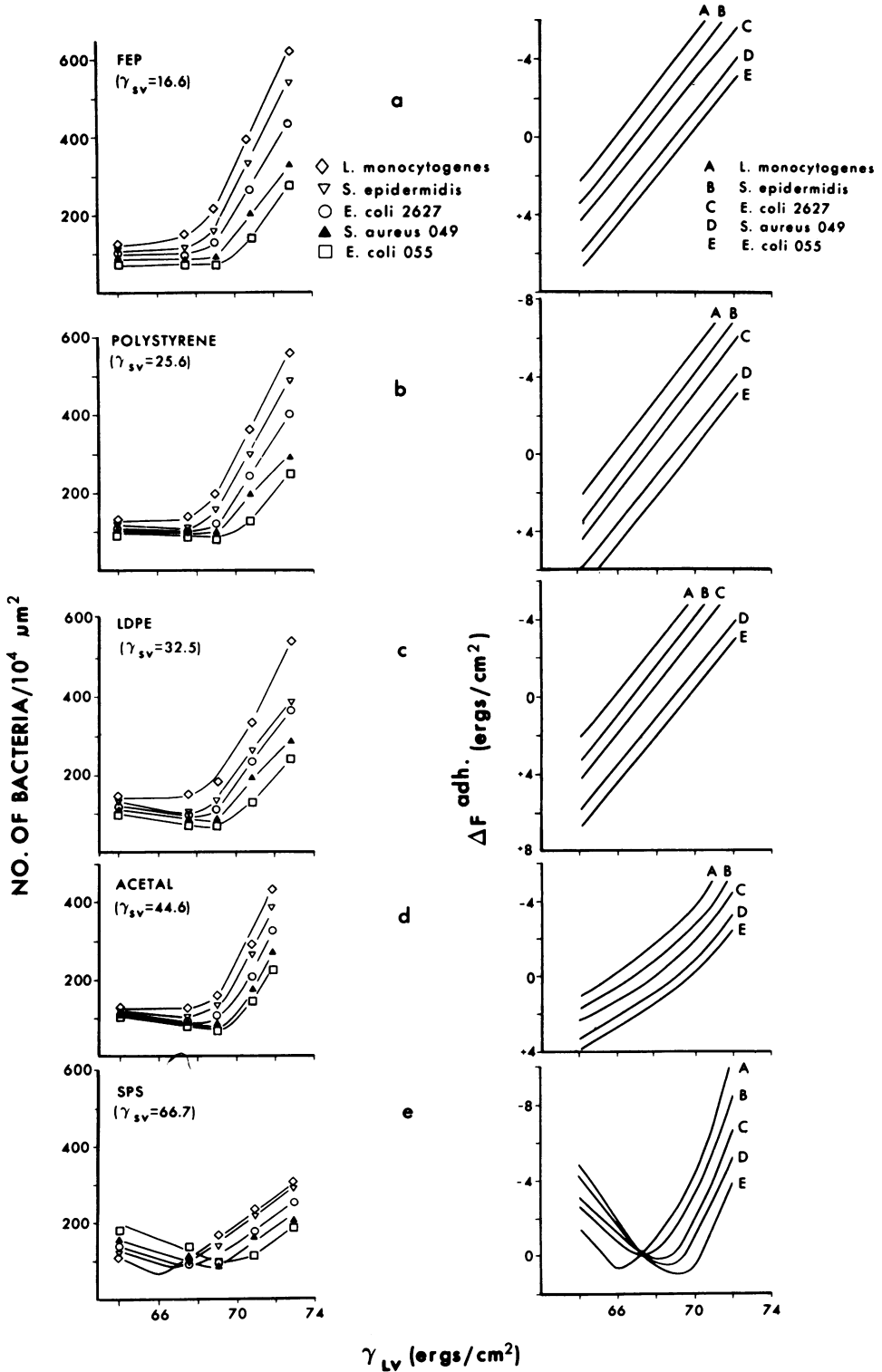


FIG. 6. Free energy of adhesion (ΔF^{adh}) as a function of the surface tension γ_{LV} of the suspending aqueous media for the five species of bacteria (right-hand side) and the experimentally determined extent of the bacterial adhesion under the same conditions (left-hand side). Errors are similar to those indicated in Fig. 3. FEP, Fluorinated ethylene-propylene copolymer; LDPE, low-density polyethylene; acetal, acetal resin; SPS, sulfonated polystyrene.

all extent of bacterial adhesion, giving rise to a certain constant level of adhesion (due to electrostatic interactions) to the various polymer surfaces.

At this point it is pertinent to note that the second prediction of the thermodynamic model under these conditions, i.e., $\Delta F^{\text{adh}} > 0$, is substantiated by the experimental results. That is, the relative order of bacterial adhesion is maintained with the most extensive adhesion being exhibited, in all cases, by the most hydrophobic bacteria for all of the liquid surface tensions, γ_{LV} , examined.

Conclusions. (i) Adhesion of bacteria to polymeric substrata, from aqueous suspensions, follows the thermodynamic model to a considerable extent. The observed pattern of bacterial adhesion is similar to that reported previously, e.g., for the adhesion of granulocytes and the adsorption of proteins, suggesting that these thermodynamic patterns of behavior are quite general.

(ii) The determination of the extent of adhesion of bacteria to polymeric substrata provides a method for the determination of the surface tension of the various bacterial species. The bacteria studied here were all found to be relatively hydrophilic, with surface tensions in the range of mid- to high-60's (ergs/cm²). The surface tension values obtained from bacterial adhesion are in good agreement with the values obtained from direct contact angle measurement on layers of bacteria as well as those obtained from phagocytic engulfment studies of bacteria by granulocytes or platelets.

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