Current Opinion in Colloid & Interface Science 15 (2010) 184–195

Contents lists available at ScienceDirect

Current Opinion in Colloid & Interface Science

journal homepage: www.elsevier.com/locate/cocis

Progress in electrohydrodynamics of soft microbial particle interphases

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ARTICLE INFO

Article history:
Received 8 June 2009
Received in revised form 2 December 2009
Accepted 4 December 2009
Available online 13 December 2009

Keywords:
Electrophoresis
Soft particles
Microorganisms
Bacteria
Viruses
Yeast cells
Heterogeneous biological interphase
Adhesion

ABSTRACT

Electrokinetic phenomena, such as electrophoresis, are valuable tools for determining the interfacial (double layer) properties of colloidal particles. The theoretical formalisms employed to interpret electrokinetic data (electrophoretic mobility) were initially derived for the restrictive case of hard (non-permeable) particles with the electrokinetic potential as unavoidable primary variable. In this paper, we underline the inadequacy of such models for addressing the electrostatic and hydrodynamic characteristics of microbes like bacteria, viruses or yeast cells. These bioparticles are characterized by heterogeneous, soft, permeable interphases formed with the outer electrolytic medium, which requires advanced electrokinetic analyses where the concept of zeta-potential must be abandoned. We review the progresses made in the measurement and analysis of interphasial properties of bioparticles under electrokinetic conditions. In particular, emphasis is given on the necessity to couple appropriately interpreted electrokinetics with other physico-chemical measurements (*e.g.* issued from AFM imaging/force spectroscopy) and microbiological techniques (genetic manipulation of microbes). Using such a combination, a clear connection between complex interphase properties of microbes and *e.g.* their propensity to adhere onto charged surfaces should be achieved.

1. Introduction

Microorganisms, or microbes, are minute organisms with sizes ranging from the nanometer to sub-millimeter scale. They are a ubiquitous life form on earth and include *e.g.* bacteria, fungi or archaea. Some microbiologists also include viruses even though others consider these as non-living. Microbes play a crucial role in all parts of the biosphere where there is liquid water, including soil, oceans and atmosphere, sometimes under extreme conditions of temperature and pressure. They are vital for recycling nutrients in ecosystems because they act as decomposers, and are further essential parts of carbon, oxygen, or nitrogen cycles. Microorganisms also play a fundamental role in the food chains as precursor links. In different contexts, microorganisms are extensively used in modern technologies based on genetic engineering, in biotechnology and food-processing industry. For the sake of examples, they are implicated in the synthesis of molecules for medical applications (vitamins, antibiotics, and enzymes) or the production of staples (cheese, beer, and yogurt). In addition, microbial communities are found in a wide range of human habitats, from skin, oral cavity to gut. Their essential role in maintaining human life and health is now well-established, and so is their sometimes disastrous impact on human health integrity with, as illustrations, the well-known epidemics that have marked human history (plague, malaria, and AIDS). One of the most predominant forms of life for microbes involves surface colonization leading to a complex three-dimensional consortium, usually called biofilm, which consists of a highly organized layer of matrix-embedded microbial populations [1]. This allows microbes to survive in hostile environments, and biofilms generally constitute protective locations from where microbes may disperse again for colonizing new niches. From this brief overview, it should be clear that the more we learn about microorganisms, the more we can both minimize their harmful potential and exploit their numerous potentialities for all kinds of applications.

Interfacial properties of bioparticles like bacteria are of utmost importance in controlling interfacial phenomena such as microbial adhesion, biocorrosion, bacterial infection or biofilm formation. The interactions of microbes with their close environment involve often intertwined biological and physico-chemical processes that are difficult to identify and quantify from molecular up to colloidal scales. Since the discovery of microorganisms in 1675 by Anton van Leeuwenhoek [2], microbiologists have largely contributed in elucidating the intimate relationship between biochemical composition of membrane, surface structure of microbes and their ability to provoke disease, to adhere onto substrate or to infect host cells. In this respect, the application of genetic and molecular methods has revolutionized all aspects of microbiology [3] over the past 50 years. In particular, genetics has been extensively used to turn off/on a specific gene in order to identify its function and related impact on the macroscopic

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doi:10.1016/j.cocis.2009.12.002

behavior of microbes. Following such a strategy, several genes and their resulting expression have been identified as key factors in *e.g.* biofilm formation [4], or surface colonization [5]. These analyses are necessarily required for increasing our understanding of microbial reactivity on biochemical and genomic levels. However, they do not provide quantitative information on the basic microbial surface/interface properties such as electrostatic charge, and the related interaction forces involved *e.g.* in the approach of a microbe toward a surface to be colonized. These latter aspects are generally tackled by physical-chemists/colloid scientists and, unfortunately, are often apprehended without full integration of the aforementioned competence developed by microbiologists in the field of genetic manipulation of microbes. In the past 20 years, many studies performed for defining the surface properties of bacterial systems derived from macroscopic and averaging measurements. Such approaches often suffered from overlooking the intrinsic relationships that exist between bioparticles behavior and the complexity of their interface as connected to *e.g.* chemical and structural heterogeneities, mechanical and hydrodynamic softness and even biological adaptation mechanisms.

Given these elements, the measurement and modeling of interfacial properties for microorganisms, as well as the understanding of microbial envelop dynamics, remain very challenging. These studies should *in fine* lead to consistent physico-chemical and biophysical descriptions of microbial interfaces at different scales, from the molecular compounds of the cell membrane to cell population interactions. In this paper, we review recent progress on the measurement and analysis of surface properties of microbial particles as derived from electrokinetic (or electrohydrodynamic) methods, namely electrophoresis. Emphasis is given on the articles published in the last ten years. In particular, the limits and benefits of electrokinetic investigation of microbes will be illustrated by invoking recent studies on bacteria, yeast cells and viruses. In addition, we shall underline the peculiarities of the interfacial (electrokinetic) properties for such bioparticles and stress their basic differences with those measured on traditional colloidal systems like latex particles or other inorganic materials. Accordingly, we give a critical discussion on the applicability of traditional electrokinetic formalisms, physico-chemical interaction models and other colloidal measurements that have been largely employed in the past for capturing the surface properties of bacteria and predicting their *e.g.* electrostatic interaction with charged substrates. Last, we shall not discuss in this review electrokinetics of macroscopic microbial surface properties, *e.g.* solid surfaces covered by microbes. It is anticipated that electrosurface phenomena like streaming current and streaming potential could be very fruitful in determining the electrostatic features of such complex surfaces on the premise that interpretation solidly includes aspects related to multi-dimensional heterogeneity in microbial population distributions along the supporting surface.

2. On the limits of standard theories for hard colloids to interpret properties of soft microbial interphases

Electrokinetic measurements on colloidal particles moving in a liquid under the action of an applied electric field (electrophoresis) may provide – pending accurate interpretation – precious information on the electric and hydrodynamic properties of the system under consideration. Over the years, substantial progress has been made in the field of electrokinetics with respect to both its theoretical and applied aspects. Such progress concerns not only the understanding of basic issues, such as the definition, measurement and interpretation of electrokinetic potentials, but also the role played by surface conduction in governing electrokinetic properties of hard, *i.e.* impermeable, colloids. It may be stated that for 'simple' surfaces, the slip process, and for that matter, the concept of zeta-potential (or electrokinetic potential), are now well-established even though molecular interpretation of *e.g.* 'stagnant layers' is an ongoing research field, in particular in the physicists community.

Electrokinetics of microbial particles, as those schematically depicted in Fig. 1, is by far less clear. The difficulty first resides in defining the nature of the very 'interface' formed between the microbe and the outer electrolyte solution. This definition is most crucial since this interface or part of it should be probed by lateral flow under electrokinetic conditions. In this regard, the major advances done in surface science instrumentation in the last decades have significantly increased our ability to explore *ex-situ* or *in-situ* microbial surface structures. Originally, the three-dimensional structures of the envelope surrounding microbes were resolved by transmission electron microscopy with or without the newer freeze-substitution cryotechniques. In case of bacteria, this methodology

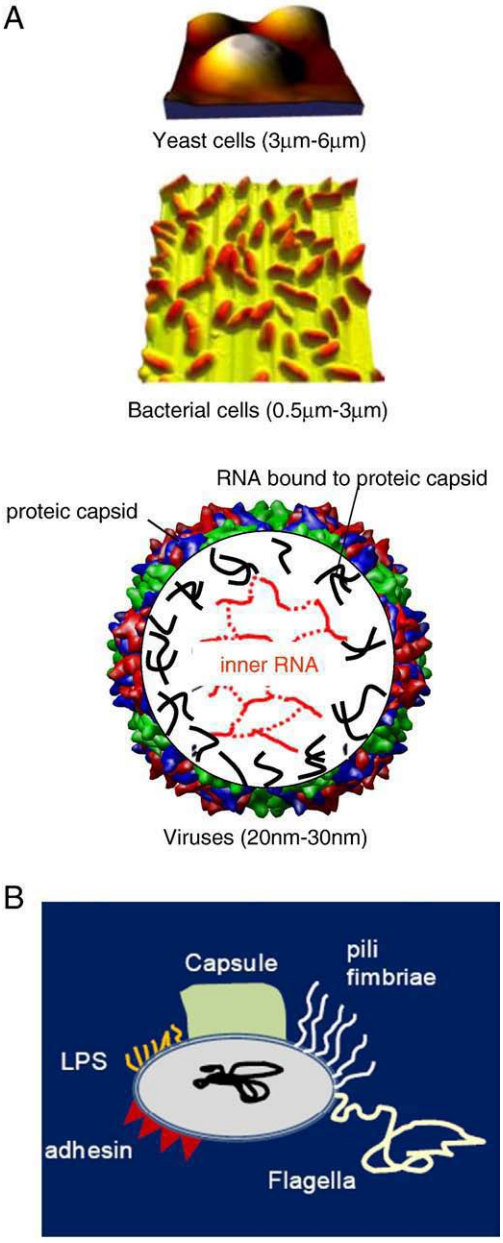

Fig. 1. (A) Representatives of microbial particles. (B) Schematic illustration of soft surface layer organizations above bacteria cell wall.
The AFM image of yeast cells is reproduced with permission from Karreman, R.J., Dague, E., Gaboriaud, F., Quilès, F., Duval, J.F.L., Lindsey, G.G. Biochimica et Biophysica Acta — Proteins and Proteomics 2007;1774: 131–137. The proteic capside of (MS2) virus is reproduced from VIPER (VIrus Particle ExplorerR) database accessible via the internet http://viperdb.scripps.edu.