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Maintaining gut ecosystems for health: Are transitory food bugs stowaways or part of the crew?

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ABSTRACT

Do food ecosystems feed gut ecosystems? And if so... fuel the immune system? Recent developments in metagenomics have provided researchers tools to open the “black box” of microbiome science. These novel technologies have enabled the establishment of correlations between dysbiotic microbial communities and many diseases. The complex interaction of the commensal microbiota with the immune system is a topic of substantial interest due to its relevance to health. The human gastrointestinal tract is composed of an immense number of resident and transient microorganisms. Both may play a direct and vital role in the maintenance of human health and well-being. An understanding of the interactions and mechanisms through which commensal and food-derived microbes shape host immunity and metabolism may yield new insights into the pathogenesis of many immune-mediated diseases. Consequently, by manipulating the contribution of food microbiota to the functionality of the gut ecosystem, there is great hope for development of new prophylactic and therapeutic interventions. This paper presents some insights and comments on the possible impact of exogenous fermented food microbes on the gut homeostasis. We shed light on the similar features shared by both fermented food microbes and probiotics. In particular, the key role of microbial strains as part of food ecosystems for health and diseases is discussed through the prism of fermented dairy products and gut inflammation.

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1. Introduction

Hippocrates of Cos (460–370 BC) stated the aphorisms that “all diseases begin in the gut”, “bad digestion is the root of all evil”, and “death sits in the bowels”. Hippocrates, known as the Father of medicine, anticipated 25 centuries ago the importance of the gastrointestinal system to human health and disease. Traditional enteric research did not heed his advice, and instead has focused on pathogenic microorganisms entering the body, mostly throughout contaminated food and beverages, to induce various diseases. Hippocrates initially affirmed the importance of food for maintaining and promoting health by claiming, “Let the food be thy medicine and medicine be thy food”. More recently, The French lawyer and politician, Anthelme Brillat-Savarin, (1755–1826) by writing, “Tell me what you eat and I will tell you what you are”, anticipated the microbiome science. Nowadays, considering the obvious role that the gut microbiome plays in shaping health and disease and the immense number of food microbes, the old saying, “You are what you eat” is still relevant. But perhaps the more relevant statement has now become, “You are what you host” (Heintz and Mair, 2014).

Microorganisms are everywhere. Microorganisms reside both outside and inside the body and include bacteria and even fungi. These

microorganisms interact with the mucosa and epitheliums of their host. The highest microbial density on earth is inside the colon, containing roughly 10^{14} microbial cells in humans. Given that the gut microbiota represents approximately 10 times the total number of human cells, a human's body should be viewed as both a complex ecosystem and symbiotic superorganism. Notably, the gut microbiota is essential for the development of intestinal immune system and for overall gut homeostasis. Consequently, the continuous commensal-host interactions profoundly affect the regulation of host metabolism. While excessive host immune stimulation by commensal or exogenous microbes can lead to inappropriate activation of immune cells and harmful intestinal inflammation, alterations of the gut microbiota have also been shown to initiate various immune-mediated diseases and metabolic disorders.

Recent developments in metagenomics have provided researchers with the tools needed to open the “black box” of microbiome science. These novel technologies have enabled the establishment of correlations between dysbiotic microbial communities and many diseases. However, despite certain studies demonstrating that some phenotypes could be communicable following microbiota transplant, clear mechanistic understanding of these phenomena is lacking (Hanage 2014; Pluznick 2014). Consequently, it is still uncertain whether these observations represent a cause-and-effect relationship. Extended approaches and meticulous data interpretation will be important for resolution of these discrepancies. Nevertheless, the complex interaction of the

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commensal microbiota with the host immune system is a topic of substantial interest for the maintenance of human health. An understanding of these interactions and the mechanisms through which commensal and food-provided microbes shape host immunity and metabolism may yield new insights into the pathogenesis of many immune-mediated diseases (Erturk-Hasdemir and Kasper, 2013). Hopefully, future findings will lead to the identification of novel prophylactic and therapeutic interventions.

This paper presents some insights and comments on the possible impact of exogenous fermented food microbes on gut homeostasis. We note the lessons that can be applied to fermented microbes from previous studies of probiotics. The key role of microbial strains as part of food ecosystems for health and diseases is discussed through the prism of fermented dairy products and gut inflammation.

2. The historical use of fermented products: a long-life coexistence of food microorganisms and gut ecosystems

2.1. Historical context

Fermented dairy products have been incorporated in the human diet since Neolithic times. This claim is supported by European archeological evidence of a pottery piece that functioned as a sieve used to make cheese approximately 7000 years ago (Salque et al., 2013). Similarly, organic masses from Early Bronze Age China in Xiaohu cemetery tombs were determined to be kefir cheese by quantitative proteomics. This cheese was likely made from skimmed ruminant milk, not curdled by ruminant rennet. This finding was the first material evidence for a lactose-free scalable “probiotic” dairy product in East Eurasia (Yang et al., 2014). Other records indicate that humans were consuming soured milks since at least 2000 years ago (Naidu et al., 1999). Fermentation is one of the oldest and most economical methods for food preservation. Fermentation also produces satisfying flavors, aromas, and texture. For centuries, fermented foods and beverages (including pickled vegetables, sauces, meats, yogurts and cheeses) have accompanied human evolution. It will be interesting for future studies to model how gut ecosystems adapt and evolve with changes to their human niche.

The increasing incidence of both autoimmune and allergic diseases in Western countries and more recently in developing countries has typically been explained by the hygiene hypothesis. However, an extension to this theory suggests that changes in the microbiota, caused by lifestyle choices and practices (e.g. diet and/or exercise) or antibiotic usage, may exacerbate inflammatory diseases such as inflammatory bowel diseases (Okada et al., 2010). Microbiota-associated perturbations provide a better explanation for the increased incidence of autoimmune diseases than genetic polymorphisms. However, the latter may emphasize the susceptibility to dysbiosis. Petrof and colleagues wisely suggested that various modern practices such as: caesarian versus vaginal delivery, formula child versus breast feeding, wide spread antimicrobial use, systematic refrigeration of foods, consumption of chlorinated water, and refined dietary foods, rarely fermented (and often grown with antibiotics) could all contribute to a loss of gut microbial richness and diversity (Petrof et al., 2013).

Medicinal and health properties of fermented foods and non-filtered beverages (wine, or beer) have been noted in many ancient texts, comprising highly biodiverse, rich and more or less controlled ecosystems, based on backslapping. Pliny the Elder, the Roman historian and philosopher, recommended the use of fermented milk to treat gastrointestinal infection. The beneficiary health effects of food microbes and fermented milk products were further popularized by Henry Tissier and Elie Metchnikoff (Metchnikoff, 1907). Given differences in culture, socioeconomics, strain origins, and methods of fermentation, fermented food microbes frequently vary in terms of their ability to limit the growth and survival of pathogenic microflora. Nowadays, attention has been given to standardizing microorganism strains and cultivation protocols used in fermentation processes in order to improve food safety and

enhance health benefits (Borresen et al., 2012; Ceapa et al., 2013). Fermented foods and beverages frequently use “domesticated” starters, which are simplified ecosystems to ensure quality control of food production. However, this modernized approach contradicts the observations that traditional cheeses have rich and diverse microbiota with high health potential (Montel et al., 2014; Bourdichon et al., 2012). Some strains from these food microbial communities have been selected as probiotic strains and successfully been incorporated into the global food production industries (Kumar et al., 2014; Foligné et al., 2013; Forstner et al., 2011).

The impact of food-associated microbes on human health involves both potential risks and benefits. Indeed, foodborne diseases encompass a wide spectrum of illnesses caused by many pathogenic microorganisms. Ingestion of foodstuffs, contaminated by hazardous microbes, is still a public health problem worldwide (Tauxe et al., 2010). On the other hand, beneficial microbes, which have been provided in fermented products for centuries (or throughout designed dietary supplements in the last few decades), may offer various ways to positively impact human health. Thus, fermented food products and probiotics should play an important role in the human diet as “functional” foods (Stanton et al., 2005; Leroy and De Vuyst, 2014; Foligné et al., 2013). All microorganisms that enter the human digestive tract must survive the acidity of the stomach environment and bile salts and enzymes of the small intestine in order to reach the colon. These survivors will then “transiently” become part of the gut ecosystem and face the challenges associated with having to cope with the intestinal mucosa, resident gastrointestinal microbes, and the host innate and immune system. Ingested microbes may impact gut homeostasis and immune equilibrium by interacting with luminal compounds, physically interacting with host cells, or through their intrinsic surface and via the secretion of bioactive molecules due to their metabolic activities. Transient microbes have the potential to interfere with the composition of the commensal core microbiota in terms of richness and diversity, metabolite production and immune signaling for further influences on host physiology (Albenberg and Wu, 2014). However, the specific contribution of food microbes to the human gut ecosystem functionality still remains unclear. Consequently, it is crucial to determine how diet(s), fermented foods, and food-derived microorganisms can influence the host microbiota, local and systemic immune responses, and overall health, either directly and/or indirectly.

2.2. Food microbes and gut microbiota as interplaying ecosystems

The composition of intestinal microbiota is highly diverse among individuals in terms of *genus* and *species*. However, the intestinal microbiota is dominated by four main phyla: Firmicutes, Bacteroidetes, Actinobacteria, and Proteobacteria. A dominant microbiota represents 10^9 to 10^{12} CFU/g of feces, while a sub-dominant microbiota ranges from 10^6 to 10^8 CFU/g. In addition, a non-negligible portion of the gut microbiota is transitory bacteria. These microbes subsequently colonize the saliva and then gut, only to disappear after several hours due to fecal elimination. Transient or “visiting” microorganisms, provided mostly through food, can reach 10^{10} to 10^{11} viable bacteria ingested per day, depending on the dietary habits and geographic areas. Indeed, fermented food and beverages can represent 5% to 40% of daily food intake (corresponding to 50 to 400 g) in certain populations (Tamang and Kailasapathy, 2010). Consequently, fermented foods are a major source of transient bacteria, corresponding to 0.1% to 1.0% of the commensals present in the gastrointestinal tract. Fermented food microbes encompass a huge diversity of Gram positive bacteria spp. from Firmicutes (such as Lactobacilli, Lactococci, Streptococci, Enterococci, Carnobacteria ...) and Actinobacteria (Bifidobacteria, Brevibacteria, Propionibacteria, ...); various Gram negative genera and species from Proteobacteria (Hafnia, Halomonas, ...); and also yeast and fungi (Kluyveromyces, Debaryomyces, Penicillium, ...). As an example, Emmental cheese can contain 10^9 *Propionibacterium freudenreichii*/g.

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