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Microbiota and lifestyle interactions through the lifespan

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ABSTRACT

Background: The human intestinal microbiota is an adaptive entity, being capable of adjusting its phylogenetic and functional profile in response to changes in diet, lifestyle and environment. Providing the host with functions important to regulate energetic homeostasis and immunological function, the gut microbiota is strategic to keep metabolic and immunological homeostasis during the entire lifespan.
Scope and approach: In the present work we review studies exploring human gut microbiota variations at different age, describing the trajectory of ecosystem changes during the course of our life, from infancy to the old age. Gut microbiota variation mirroring subsistence strategy is also explored, with a particular focus on how the gut microbiota changes in response to modifications in the diet. Finally, we illustrate how an abnormal dietary intake could force microbiota to an obese-associated configuration, which concurs in compromising the host metabolic homeostasis.
Key findings and conclusions: Our work allows appreciating the importance of the physiological flexibility conferred by the microbiota for modulating our metabolic and immunological phenotype along the course of our life. Further, the key role of the gut microbiota in providing an extra means of adaptive potential during our evolutionary history is highlighted, suggesting the importance of the intestinal microbiota-host interplay for the maintenance of human health and homeostasis in changing environments. On the other hand, different lifestyle and dietary factors, such as sanitization and antibiotic usage or high-fat diet, can force maladaptive changes in the microbiota configuration which could have negative effects on human health. Thus, it is important to modulate diet and lifestyle habits to keep a mutualistic gut microbiota layout along the course of our life.

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1. The human intestinal microbiota

The human gut harbors a complex and dynamic ecosystem of microbes – the gut microbiota – that live in close and intimate relationship with the host, and have a large impact on several aspects of our physiology. This abundant microbial community includes members of all three domains of life: Bacteria, which predominate, Eukarya and Archaea, up to 10^{14} microbial cells (Oxley et al., 2010; Scanlan & Marchesi, 2008 and Turnbaugh et al., 2007). The gut microbiota is composed of relatively few bacterial phyla, with Firmicutes and Bacteroidetes accounting for >90% of the resident microorganisms (Eckburg et al., 2005), but it is notable for its species and strain level diversity, with thousands of species detected in the gut of the human population and approximately 160 prevalent species per individual (Qin et al., 2010) This peculiar structure at lower phylogenetic levels varies dramatically from one individual to the next, with only a small phylogenetic overlap between people (Qin et al., 2010, Tap et al., 2009), and can change quickly over time in a single individual under environmental and endogenous pressures (Candela, Biagi, Maccaferri, Turroni, & Brigidi, 2012 and Faith et al., 2013).

Encoding 10 million non-redundant microbial genes – 400-fold more than the human gene complement – the gut microbiota is widely recognized as an integral and active organ of the human body, which provides functions indispensable to our life (Qin et al., 2010). Intestinal microbes produce indeed essential vitamins, and have the potential to metabolize a wide range of dietary substrates in a complex and intense microbiota-host transgenomic metabolism, deeply influencing our energy and metabolic homeostasis

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(Nicholson et al., 2012 and Rakoff-Nahoum, Coyne, & Comstock, 2014). In particular, the extraordinary diversity and abundance of carbohydrate-active enzymes represented in the gut microbiota complement the poor human glycobiome repertoire (El Kaoutari, Armougom, Gordon, Raoult, & Henrissat, 2013), allowing the extraction of energy from otherwise indigestible polysaccharides, breaking down dietary fiber into adsorbable short-chain fatty acids (SCFA) (Flint, Duncan, Scott, & Louis, 2015). These major products of carbohydrate fermentation, acetate, propionate and butyrate, have a critical role in shaping the host nutritional status, controlling energy production, storage, and appetite (Kimura et al., 2013; Samuel et al., 2008; and De Vadder et al., 2014). SCFA are also crucial in keeping immune homeostasis, acting both locally in the gut and remotely at other organs, thus supporting the strategic role of microbiota in promoting and maintaining a balanced immune response in the course of human life, from infancy to adulthood (Arpaia et al., 2013; Kamada, Seo, Chen, & Núñez, 2013 and Smith et al., 2013a,b). According to an increasingly large body of evidence, although almost all limited to mice, the microbes in our intestines may also have a major impact on our state of mind, through a bidirectional gut brain axis, governing anxiety and mood disorders (Schmidt, 2015).

2. Impact of lifestyle on the assembly of gut microbiota during infancy

The relationship between microbes and human host in the intestine starts at birth. At birth, human beings are sterile and, since their first day of life, they are readily colonized by a pool of microorganisms coming from the mother (vaginal microbiota and fecal microbiota), from mother milk microbiota and from the surrounding environment. During the first months of life the infant gut microbial ecosystem is in continuous variations in terms of composition, and in breast-fed infants is largely dominated by *Bifidobacterium* showing *Enterobacteriaceae* as second dominant group. Thus, since our birth, a huge quantity of different microorganisms interact with the intestinal epithelial cells and the gut associated lymphoid tissue (GALT), generating a dense network of intercommunications, which probably constitutes the prerequisite for the development of the immune and metabolic homeostasis later in life (Koenig et al., 2011; Mueller, Bakacs, Combellick, Grigoryan, & Dominguez-Bello, 2015 and Palmer, Bik, DiGiulio, Relman, & Brown, 2007). The diversity and variation of the host–bacteria interactions along our infancy, and, most important, the establishment of a mutualistic developmental gut microbiota trajectory in early life, have been hypothesized as a key factor for the healthy development in childhood (Bisgaard et al., 2011; Cox et al., 2014). Several studies suggest that a shrinkage of the gut microbiota-host interactions at infancy by lifestyle practices (caesarean section, antibiotic use, formula feeding of infants) could compromise the mutualistic process of gut microbiota assembly, increasing the risk of allergic and metabolic diseases later in life (Conradi et al., 2013; Cox et al., 2014; Marra et al., 2009; Fung, Garrett, Shahane, & Kwan, 2012; Risness et al., 2011 and Tenconi et al., 2007). This concept was pioneered by the hygiene hypothesis (Strachan, 1989), which has connected for the first time a reduced microbial contact at early age, as a result of increase of hygiene practices in the Western world, to the growing epidemic of atopic eczema, allergic rhinoconjunctivitis and asthma among Western people (Blaser & Falkow, 2009; Noverr & Huffnagle, 2005 and Rautava, Luoto, Salminen, & Isolauri, 2012).

The evidence in favor of the hygiene hypothesis has paved the way to comparative studies between Western and non-Western infants, to identify the effect of different subsistence strategies and hygienic practices on the process of gut microbiota assembly. In particular, the comprehension of the factors that drive the microbiota assembly across human populations with different subsistence strategies is mandatory to extract the impact of Westernization on such process. In this perspective, the establishment of the human microbiota needs to be conceived as a co-evolution trajectory, resulting from a combination of forces that are the assortment of interactions within the bacterial community, the history of assembly (dynamics of the microbial composition) and habitat conditions (diet and interactions with the human host) (Nemergut et al., 2013). In a first milestone study, a loss of gut microbiota diversity in Italian children respect to rural Burkina Faso ones was observed (De Filippo et al., 2010). In particular, the firsts completely lacked *Prevotella*, *Xylanibacter* and *Treponema* genera. The higher microbial diversity of African children has been connected to their high-fiber diet since weaning and a larger exposure to environmental microbes. In another work, the microbiota of US babies has been compared to rural Malawians and Amerindians, confirming a different taxonomic structure of the microbiota among rural and urban populations during the first 3 years of life (Yatsunenko et al., 2012). Interestingly, a metagenomics analysis of the same samples has identified a significant overrepresentation of genes involved in the catabolism of breast milk polysaccharides and intestinal mucosa glycans (mannans, sialylated glycans, galactose and fucosyl saccharides) in Amerindian and Malawian babies respect of the USA ones, probably mirroring differences in the quality of breast milk between the three populations and suggesting a closer interaction between bacteria and intestinal epithelial cells in rural infants (Yatsunenko et al., 2012). These findings have opened the way to further in-depth pioneering analyses, aimed to specifically investigate the effect of the mother diet during pregnancy and breast-feeding on the infant microbiota assembly (Gueimonde et al., 2006; Lahtinen et al., 2009 and Ismail et al., 2012).

Taking together, these studies demonstrate that different lifestyle strategies can affect the microbiota assembly in identifiable ways along our infancy, according to the mother and infant diet and the interactions with the bacteria from food and environment. Interestingly, independently from quality of feeding and geographical origin, a healthy developmental trajectory of the infant gut microbiota shows conserved traits, as the progression from microbes that utilize human homopolysaccharides to produce lactate, such as *Bifidobacterium*, during the lactation period, to microorganisms associated with a solid diet (Koenig et al., 2011). Furthermore, the diversity of the infant microbiota progressively increases in the early development, reaching a maximum between 3 and 5 years of age, depending on the subject (Kostic et al., 2015; Murgas Torrazza & Neu, 2011 and Palmer et al., 2007). Interestingly, impairments or delays in the microbiota assembly during infancy have been associated with some extreme cases of severe acute malnutrition, compromising the formation of the adult-like microbiota structure (Subramanian et al., 2014, Smith et al., 2013a,b). In a first illuminating study, severe acute malnutrition in children from Bangladeshi has been associated with significant microbiota immaturity, which could be only partially ameliorated with nutritional intervention (Subramanian et al., 2014). In particular, the microbiota of malnourished children (age: 6.5–26 months) showed high levels of bacteria belonging to *Enterobacteriaceae* family and *Streptococcus* genus, which are opportunistic pro-inflammatory bacteria, and low levels of immune-modulatory *Bifidobacterium*. Furthermore, their microbiota did not show the progressive increases of *Faecalibacterium*, *Clostridium* and *Ruminococcus* genera, concomitant bacterial groups with the weaning period in healthy children and pivotal for the development of the adult-like structure (Subramanian et al., 2014). Similarly, in another well-structured work, the effects of Kwashiorkor,

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