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COMMENTARY AND VIEWS

Do microbiotas warm their hosts?

Eugene Rosenberg[a] and Ilana Zilber-Rosenberg[b]

[a]Department of Molecular Microbiology and Biotechnology, Tel Aviv University, Tel Aviv, Israel; [b]Independent scientist, Givat Shmuel, Israel

ABSTRACT
All natural animals and plants are holobionts, consisting of a host and abundant and diverse microbiota. During the last 20 years, numerous studies have shown that microbiotas participate in the ability of their hosts to survive and reproduce in a particular environment in many ways, including contributing to their morphology, development, behavior, physiology, resistance to disease and to their evolution. Here we posit another possible contribution of microbiotas to their hosts, which has been underexplored - the generation of heat. We estimate that microbial metabolism in the human gut, for example, produces 61 kcal/h, which corresponds to approximately 70% of the total heat production of an average person at rest.

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Microorganisms, like all cells, produce heat as a by-product of the enzymatic catabolism of substrates and synthesis of cell material. When expressed per unit weight, a microorganism produces more heat than any other organism.[1] The amount of heat generated by bacteria depends on the growth substrate, growth rate and growth stage.[2] In general, heat production is inversely proportional to growth rate: the faster the growth, the lower the rate of heat production per unit weight. Using micro-calorimeter measurements, it was reported that *Bacteroides ruminicola*, reclassified as *Prevotella ruminicola*,[3] grown anaerobically with glucose as a substrate has specific rates of heat production of 135 milliwatts (mW)/g (dry weight) and 247 mW/g at doubling times of 2.5 h and 4 h, respectively.[4] Considering the average doubling time of bacteria in the mammalian gut to be 2.7–2.9 h,[5] the predicted heat production would be 168 ± 11 mW/g bacteria. This is close to the value (170 mW/g bacteria) reported for *Streptococcus bovis* growing anaerobically on glucose.[6]

Since 1 W = 0.24 cal/sec, the average estimated heat production of gut bacteria, 168 mW/g, would equal 0.0403 cal/sec per g bacteria. Thus, the human colon's resident bacteria, corresponding to ca. 300 g dry weight bacteria (NIH Human Microbiome Project 2012), would produce about 12 cal/sec, or 43 kcal/h. Assuming the heat was spread over a 70 kg person and there was no heat loss, gut bacteria would raise body temperature by about 1.0°C/h. By comparison, the total measured heat produced by a human at rest is about 1 W/kg, or 70 W for an average person,[7] corresponding to 60 kcal/h. Thus, about 70% of body heat at rest is the result of bacterial metabolism in the gut. The major sources of substrates for microbial growth and heat production in the mammalian intestines are complex non-digestible dietary carbohydrates[8] and host–derived mucins.[9]

This theoretical argument contains several assumptions, some of which were already mentioned above. Others are that gut bacteria produce heat at a rate similar to *P. ruminicola* growing slowly in an anaerobic chemostat, and that the dry weight of bacteria in the human gut, which is variable, is ca. 300 g. Regardless of the exact magnitude of the temperature rise, it is clear that microbe-generated heat contributes to maintaining body temperature in animals. Consistent with this concept are the reports that treatment of rabbits[10] and rodents[11] with antibiotics lowered their body temperature. A similar decrease in body temperature was found in germ-free mice and miniature piglets in comparison to conventionally raised animals.[12] Heat output by gut microbiota may also help explain the observation that germ-free mice had 40% less total

CONTACT Eugene Rosenberg eros@post.tau.ac.il Department of Molecular Microbiology and Biotechnology, Tel Aviv University, Ramat Aviv, Israel

body fat than conventionally raised mice, even if their caloric intake was 29% higher than that of conventionally raised animals.[13]

In ruminants, termites and other lignocellulose-degrading animals a large part of heat production is the result of microbiota, either directly from microbial metabolism or indirectly by the production of fermentation products that are used by the host for metabolic processes. It was observed that heat production in goats, after emptying the rumen of their microbiota, decreased by about 50%, suggesting that during fasting half of the heat produced by the animal was due to microbial fermentation and half to host metabolism.[14] It was also observed that the amount of heat produced by rumen microbiota is influenced by diet. Certain food additives decreased the temperature of the rumen of steers by optimizing microbial fermentation to produce more propionate and less acetate.[15] Based on these data and the fact that diet influences human gut microbiota composition,[16] we suggest that foods can have warming or cooling properties depending on what changes they bring about in the microbiota. Could this help explain the traditional Chinese medicine concept of heating and cooling foods?

To our knowledge the only published report that has considered the warming effect of microbiota in plants involved flowers of the winter-blooming herb *Helleborus foetidus*.[17] Heat produced by the sugar catabolism of yeast populations inhabiting floral nectar increased the temperature of floral nectar and, more generally, modified the within-flower thermal microenvironment. ΔT of nectars was linearly related to log yeast cell density, and reached +6°C in nectars with the densest yeast populations. The thermal effects associated with the presence of yeast in *H. foetidus* nectar are the outcome of intense fermentative–oxidative sugar metabolism, particularly when it takes place under extreme C: N imbalance,[18] as typically found in floral nectar.

In summary, heat production by symbiotic microbes is a general phenomenon because all animals and plants contain abundant microorganisms and all microorganisms produce heat. Heat the microbiota produces will combine with other sources of body heat, and in warm-blooded animals, temperature will be controlled by the well-studied feedback system. Though the significance of heat production by microbiotas has scarcely been studied, its contribution may have far-reaching implications. It may help warm-blooded animals avoid hypothermia in cold climates, and in cold-blooded animals (ectotherms), it can raise the body temperature. In this regard, it would be interesting to examine if evolution selected for microbiotas that produce more heat in animals (and may be also in humans) that live in cold environments compared to those in warm climates.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

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