

## REVIEW ARTICLE

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# Microenvironmental influences on T cell immunity in cancer and inflammation

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T cell metabolism is dynamic and highly regulated. While the intrinsic metabolic programs of T cell subsets are integral to their distinct differentiation and functional patterns, the ability of cells to acquire nutrients and cope with hostile microenvironments can limit these pathways. T cells must function in a wide variety of tissue settings, and how T cells interpret these signals to maintain an appropriate metabolic program for their demands or if metabolic mechanisms of immune suppression restrain immunity is an area of growing importance. Both in inflamed and cancer tissues, a wide range of changes in physical conditions and nutrient availability are now acknowledged to shape immunity. These include fever and increased temperatures, depletion of critical micro and macro-nutrients, and accumulation of inhibitory waste products. Here we review several of these factors and how the tissue microenvironment both shapes and constrains immunity.

**Keywords:** immunometabolism; T cell; microenvironment; cancer; inflammation

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## INTRODUCTION

The classic metabolic chart present in every biology classroom and textbook is a staple of biochemical training and represents the culmination of over a century of detailed and rigorous studies. These seminal discoveries define the landscape of fundamental chemical reactions that integrate environmental signals and nutrients to support the viability, growth, and activities of every living cell. When cells receive signals to perform specific functions such as to grow and proliferate, they adjust their nutrient uptake and shift metabolic programs to meet the new demands. If, however, adequate levels of essential nutrients are not available or if end products or waste products accumulate, basic chemistry and chemical equilibria may bring these pathways to a halt or shift their outcomes to disrupt or alter cell fates. Thermodynamic effects such as temperature changes may also influence T cells. Much the same as cell cycle checkpoints can stop or delay cell division, metabolic checkpoints thus interpret nutrients and cell energetics to determine cell differentiation, function, and fate. Cell metabolism is thus the biochemistry of how cells interpret and integrate signals from their microenvironment.

T cells and macrophage metabolism have been studied to the greatest detail in the field of immunometabolism. In addition to many studies focused on how cell activation signals can reprogram metabolism from catabolic programs designed to generate energy to anabolic programs that efficiently provide biosynthetic precursors to support cell growth and proliferation [1], it is now apparent that each immune cell type and subset has specific metabolic requirements for activation and differentiation that reflect their specific roles and demands. Importantly, the tissue

microenvironment exerts a profound influence on these processes. Cell activating signals, microenvironmental nutrients, and other conditions integrate through upregulation of nutrient transporters and the subsequent changes in intracellular nutrients influence cell bioenergetics, biosynthesis, and signaling. Metabolic signaling through generation of co-factors or posttranslational modifications can then serve to shape cell fate or activate metabolic checkpoints. These include nutrient sensing pathways such as the AMPK or mTORC1 and HIF signaling axis, stress response pathways including reactive oxygen species (ROS) and ER stress, or changes to epigenetic marks and histone modifications that regulate gene expression. These changes are broadly relevant to immunity and inflammation and may have a particularly important impact in settings such as obesity or in tumor microenvironments (TME). Here we review how key changes in systemic nutrient status as well as microenvironmental metabolites and other conditions are integrated to shape the fate of T cells.

## Micronutrients and ions

While cell metabolism typically focuses on intermediary metabolites and central carbon metabolism pathways, ions and other elements play key roles (Fig. 1A). Micronutrients such as ions have increasingly been shown to impact the adaptive immune system, particularly T cells. For example, recent literature has highlighted that potassium ( $K^+$ ) can directly influence T cells. Increased  $K^+$  ion concentration in the tumor microenvironment can acutely silence T cell effector function [2]. In contrast, high concentrations of this ion preserve T cell stemness through acetyl CoA metabolism and by epigenetically regulating gene transcription, nutrient

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# Microenvironmental Aspects Of Immunity

**RJ Shavelson**



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