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T-cell potential and development *in vitro*: the OP9-DL1 approach

Renée de Pooter and Juan Carlos Zúñiga-Pflücker

In vivo, T cells develop in the thymus from bone marrow-derived hematopoietic progenitors. Similarly, T cells can develop *in vitro* in model systems that mimic thymic function. The recent development of the OP9-DL1 cell culture system, a two-dimensional T-inductive environment, has provided greater access to the processes of commitment and development in T lymphocytes.

Addresses
Department of Immunology, University of Toronto, Sunnybrook Research Institute, 2075 Bayview Avenue, Toronto, ON M4N 3M5, Canada

Corresponding author: Zúñiga-Pflücker, Juan Carlos (jc.zuniga.pflucker@utoronto.ca)

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Introduction

Adaptive immunity protects vertebrates from infection, parasites and neoplasia, and T lymphocytes comprise a major component of this immunity. Although ultimately derived from bone marrow (BM)-resident hematopoietic stem cells (HSCs) like all hematopoietic cells, T cells are unique as they require the specialized microenvironment of the thymus to develop. Stromal-derived signals provided by this specialized organ commit the BM-derived thymus seeding progenitor (TSP) to the T lineage, and support its progeny as they negotiate various developmental checkpoints. The absolute requirement for — and the complexity of — these thymocyte–stromal interactions has necessitated the development of *in vitro* model systems to facilitate the study of T-cell development.

Until recently, T lymphopoiesis (the generation of T lymphocytes) was thought to require the three-dimensional structure of an intact thymus [1]. This led to the development of fetal thymus organ cultures (FTOCs) [2]: thymic explants that could be depleted of endogenous thymocytes and seeded with defined progenitors. FTOCs, together with reaggregate thymic organ cultures (RTOCs), in which stromal subpopulations can be disaggregated and variously recombined [3], have contributed enormously to our understanding of T lymphopoiesis and thymocyte–stromal interactions [1]. However, although powerful, these systems have some limitations: cell yields are low and seeding efficiency depends on many variables, which are not necessarily progenitor-intrinsic. In FTOCs, the requirement for migration into the thymic lobes obscures the distinction between a lack of T-cell potential and/or homing defects. Although RTOCs overcome the latter [4], the technical demands of thymic explants complicate manipulation of the progenitors during differentiation, and make single cell and progenitor frequency analyses challenging and difficult to compare with non-T lineage analyses.

However, in 2002 a complementary model system was developed that also demonstrated that T lymphopoiesis did not require a three-dimensional environment [5]. This new approach evolved from the convergence of two findings: that the OP9 macrophage colony stimulating factor-deficient bone marrow stromal line supported the differentiation of all hematopoietic lineages except T cells [6,7], and that signals via the Notch receptor, the ligands of which are expressed in the thymus [8,9], were required to induce T commitment and did so at the expense of other lineages [10]. Thus, OP9 cells transduced with the Notch ligand Delta-like-1 (OP9-DL1 cells) — one of three Delta-like mammalian Notch ligands — supported T lymphopoiesis from mouse fetal liver (FL) or BM HSCs and embryonic stem cells [5,11,12], as well as from human cord blood (CB) and BM [13,14]. Notably, in similar contexts the Jagged family of Notch ligands influence non-T cell fates, but do not support T-cell differentiation from HSCs [15,16]. By contrast, OP9-DL1 cells induce efficient T lymphopoiesis through the early $CD4^-CD8^-$ double-negative (DN) stages to the $CD4^+CD8^+$ double-positive (DP) stage, and generate functional single-positive (SP) $CD8^+$ $TCR\alpha\beta^+$ T cells [5,17]. Although $CD4^+$ cells do not arise, coculture-derived DN cells seeded into FTOCs and implanted into immunodeficient mice yield both $CD4^+$ and $CD8^+$ cells, which traffic through the periphery and respond to viral challenge [11]. Human T-cell development is supported from CB or BM $CD34^+CD38^-$ progenitors to the $TCR\alpha\beta^+$ DP stage [13,14]. CB progenitors also generate phenotypically mature $CD4^+$ and $CD8^+$ T cells, possibly selected by MHCs expressed by the progenitors themselves (JCZP, unpublished). This suggests that the absence of certain mature populations results from the absence of the appropriate selecting MHC, not from a persistent maturational defect imposed by OP9-DL1 coculture.

Essentially, OP9-DL1 cells lack the ability of FTOCs to mediate all aspects of selection, but can provide

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