

# Signal transduction by cell adhesion receptors in leukocytes

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**Abstract:** Leukocytes usually pass through the blood stream as nonadherent cells, but during an immune response and inflammation, they become adherent in order to migrate through tissues. Three families of adhesion molecules, the immunoglobulin family, the selectins, and the integrins, participate in interactions between leukocytes and tissues. Near sites of inflammation, leukocytes initially interact with the endothelium via selectins, causing them to slow down and to roll along the walls of blood vessels. Next, chemoattractants induce the activation of integrins on leukocytes. Finally, activated integrins mediate leukocyte migration through the endothelium into the inflamed site. Interactions of leukocytes with other cells and various extracellular matrix (ECM) proteins lead to different functional cell responses, including changes in growth, behavior, and differentiation. Many of these interactions are mediated by integrins, which "integrate" ECM protein signals with the cytoskeleton and which also act as true receptors that generate biochemical signals within the cell. Changes in pH, cytoplasmic  $Ca^{2+}$  concentration, phosphorylation, and gene induction have all been observed after integrin engagement. Adhesion-mediated gene induction in monocytes is perhaps the best example that integrins initiate signaling cascades in the cell to deliver information from the ECM all the way to the nucleus. *J. Leukoc. Biol.* 57: 189-198, 1995.

**Key Words:** selectins • integrins • inflammation • extracellular matrix • adhesion

## INTRODUCTION

Leukocytes are in constant movement within the body, patrolling for damage and the presence of foreign organisms. Upon activation, they begin to migrate through capillary endothelium and into the tissues. During inflammation, the different types of leukocytes leave the blood stream in an orderly fashion [1]. Recognition of inflamed sites and migration through extracellular matrix (ECM) are mediated by various families of cell adhesion receptors, the immunoglobulin family, the selectins, and the integrins [2]. These adhesion molecules act in sequence to allow leukocytes to leave the circulation. Once out of the blood vessel, leukocytes interact with ECM proteins mainly through integrins. These receptors interact with the cytoskeleton, integrating the extracellular environment with the cell interior [3, 4]. Signals from ECM proteins, transduced by integrins, also result in functional cell changes, such as cell growth, differentiation, and gene induction [5]. It is becoming clear that integrins can induce these changes by activating biochemical signaling cascades within the cell, just as other receptors do. This review briefly describes the receptor families involved in leukocyte adhesion and their role during inflammation and discusses the advances in understanding the signaling pathways from integrin receptors.

## LEUKOCYTE ADHESION RECEPTORS

Leukocytes have the important function of protecting the body against infectious organisms. To patrol the body for the presence of foreign elements, leukocytes move in the blood and lymph as nonadherent cells and migrate as adherent cells through tissues. Change between adherent and nonadherent stages is of major importance for the proper response of immune cells during infection and inflammation. Three families of adhesion molecules are known to be involved in interactions between circulating leukocytes and tissues.

### The Ig family

The immunoglobulin (Ig) family contains many molecules involved in adhesion and transmembrane signaling in leukocytes. They all contain at least one Ig domain, consisting of 70-110 amino acids, with a disulfide bridge spanning 50-70 residues that folds the domain in the typical tertiary structure present in antibodies [6]. Interleukin-1 receptor (IL-1R), ICAM-1 (ICAM-1; CD54), ICAM-2 (CD102), and ICAM-3 (CD50), vascular cell adhesion molecule-1 (VCAM-1; CD106), and mucosal addressin cell adhesion molecule-1 (MAdCAM-1) belong to this family and are expressed on endothelial cells (reviewed in ref. 2). ICAM-1 and VCAM-1 are expressed minimally on resting endothelium; in contrast, ICAM-2 seems to be constitutively present [7]. MAdCAM-1 is expressed on Peyer's patch high endothelial venules. All these Ig family members bind to ligands on leukocytes to mediate adhesion and migration, as discussed later.

### Integrins

Counterreceptors for ICAMs, VCAM-1, and MAdCAM-1 belong to the integrin family [3, 4, 8]. Members of this family mediate cell-to-cell and cell-to-extracellular matrix interactions. Integrins are plasma membrane receptors composed of two gene products,  $\alpha$  and  $\beta$  chains, which are linked in a noncovalent but very stable structure (heterodimers). Both chains are required for normal receptor expression and for ligand binding. Currently, more than 15  $\alpha$  chains and at least 8  $\beta$  chains have been characterized [4] (Fig. 1). Most  $\beta$  chains have the ability to combine with more than one  $\alpha$  chain, to make a number of heterodimers with varying func-

**Abbreviations:** CR3, complement receptor 3; ECM, extracellular matrix; FAK, focal adhesion kinase; ICAM-1, intercellular adhesion molecule-1; IL, immunoglobulin; IFN- $\gamma$ , interferon- $\gamma$ ; Ig, immunoglobulin; IL-1, interleukin-1; LAD, leukocyte adhesion deficiency; LeuCAM, leukocyte cell adhesion molecule; LPS, lipopolysaccharide; MAdCAM-1, mucosal addressin cell adhesion molecule-1; NF- $\kappa$ B, nuclear factor  $\kappa$ B; NK, natural killer; PAF, platelet-activating factor; PMA, phorbol myristate acetate; RTK, receptor tyrosine kinase; TCR, T cell receptor; TNF- $\alpha$ , tumor necrosis factor  $\alpha$ ; VCAM-1, vascular cell adhesion molecule-1.

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# Signal Transduction In Leukocytes

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