

## Cellular recognition and patterning in sensory systems



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### ABSTRACT

Cells dissociated from various tissues of vertebrate embryos preferentially reaggregate with cells from the same tissue when they are mixed together. This tissue-specific recognition process in vertebrates is mainly mediated by a family of cell adhesion molecules because of their specific binding properties. Recent studies have revealed that two families of adhesion molecules, nectins and cadherins, are associated with each other, and these associations provide cells with the differential adhesive affinities required for cellular recognition and complex cellular pattern formations during development. This review provides an overview of recent findings regarding the cooperative functions of nectins and cadherins, as well as a discussion of the molecular basis underlying these functions.

### 1. Introduction

Cells dissociated from various tissues of vertebrate embryos preferentially reaggregate with cells from the same tissue when they are mixed together. This tissue-specific recognition process in vertebrates is mediated by various cell adhesion molecules that hold cells together by homophilic or heterophilic interactions between such transmembrane proteins on adjacent cells. Some cell–cell junctions are asymmetric or heterogeneous. For example, synapses are asymmetric junctions that are usually formed between axons and dendrites, myelin is formed between neurons and supporting glial cells, and the sensory epithelium consists of heterogeneous junctions between sensory and supporting cells. These asymmetric or heterogeneous junctions are generally found in a variety of tissues and organs. Selective cell–cell adhesion between different cell types is fundamental for cell recognition and sorting different cell types in morphogenesis. Recent advances have clarified the molecular compositions of various cell interfaces and provided new insights into asymmetric or heterogeneous cell–cell recognition and junction formation. Cell–cell junctions contain various transmembrane proteins, cytoskeletal elements, and signaling complexes. A single cell type employs multiple molecular mechanisms for adherence to other cells. The specificity of cell–cell adhesion in development results from the integration of several adhesion systems. Here, we briefly review the cooperative roles of nectins and cadherins in cell recognition and adhesion during asymmetric or heterogeneous cell–cell junction formations. These mechanisms also explain the organization of highly ordered cellular patterns in complex sensory organs.

### 2. Molecular basis of cadherins and nectins in cellular recognition and adhesion

Cadherins are adhesion molecules involved in adhesion and selective cell–cell recognition of vital biological processes such as embryogenesis, pattern formation, and neural circuit formation [1]. Cadherins constitute a superfamily and are grouped into subfamilies designated as classic cadherins and proto-cadherins. The defining feature of classic cadherins is the presence of a conserved intracellular domain that mediates cytoplasmic interactions with catenins. Here, for convenience, classic cadherins are simply referred to as cadherins. Cadherin molecules associate with p120 catenin and  $\beta$ -catenin via their cytoplasmic domain, and  $\beta$ -catenin in turn binds to  $\alpha$ -catenin.  $\alpha$ -Catenin interacts with F-actin, and an interaction between the cadherin–catenin complex and actin cytoskeleton is thought to be crucial for cadherins to create firm cell adhesions (Fig. 1A) [2]. The expression patterns of multiple cadherins and their dynamic changes during development are the most fascinating features observed in the cadherin family. In mixed cultures of cell lines expressing different types of cadherins, the cells form separate aggregates according to their homophilic binding property (Fig. 1B) [3]. Through their selective adhesive property, cadherins are thought to be the main driver of various morphogenetic events [4,5]. Binding specificity of cadherins is attributed to the extracellular domain because exchange of this domain between two different cadherins determines cell aggregation and sorting specificity [6,7]. Many subtypes of cadherins are expressed by restricted groups of cells in tissue and their expression patterns

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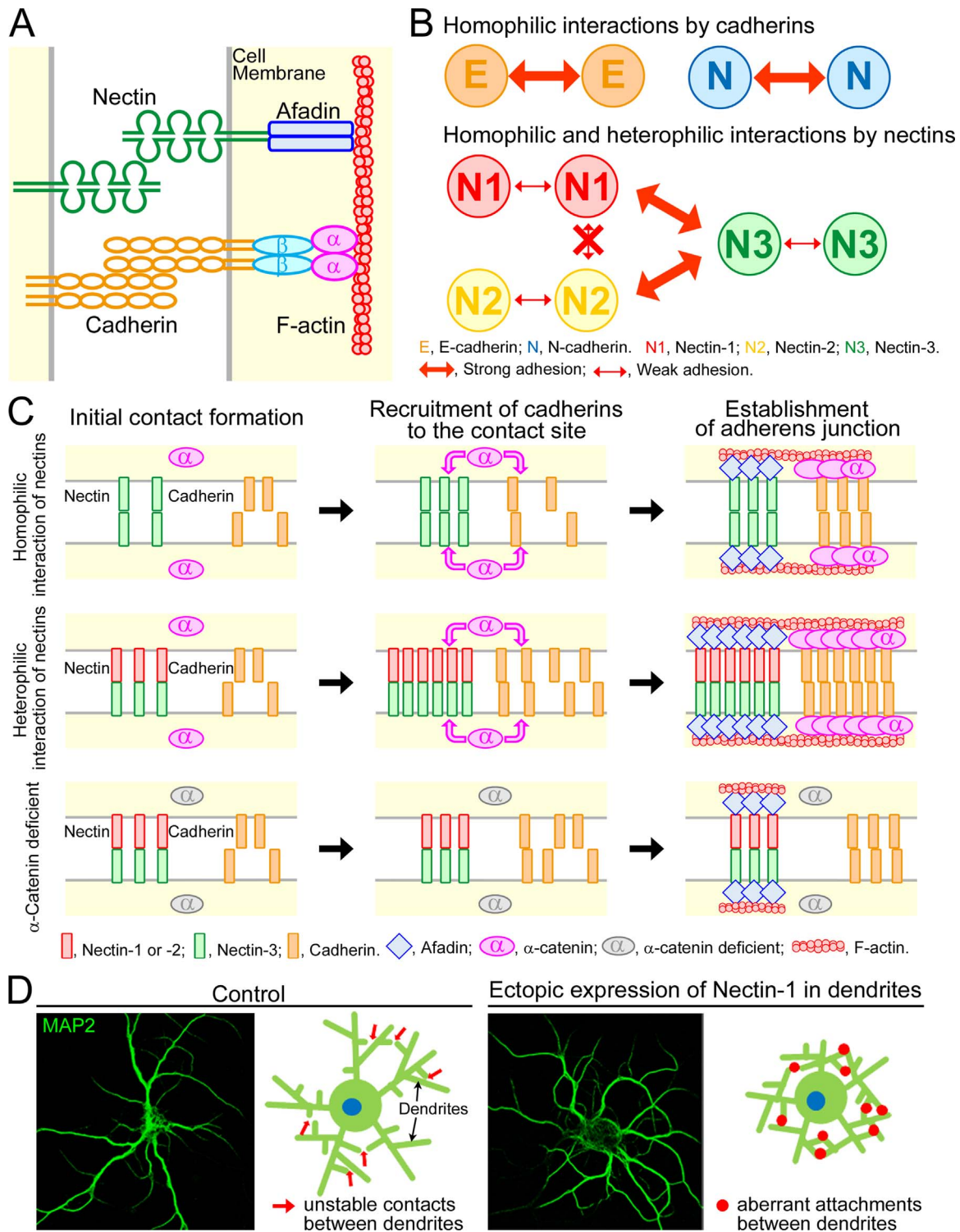
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**Fig. 1. Molecular interactions between nectins and cadherins.** (A) Molecular interactions between nectins and cadherins at the cell–cell junction.  $\alpha$ ,  $\alpha$ -catenin;  $\beta$ ,  $\beta$ -catenin. (B) Schematic illustrations of *trans*-interactions among cadherins or nectins. (Upper) Homophilic *trans*-interactions between cadherins. (Lower) Homophilic and heterophilic *trans*-interactions between nectins. (C) Association of the nectin-afadin system with the cadherin-catenin system during the formation of cell–cell junctions. (Upper) Homophilic *trans*-interactions between nectins recruit cadherins to the contact site by cytoplasmic interactions and promote the formation of adherens junction. (Middle) Heterophilic *trans*-interactions between nectins recruit cadherins intensely to the contact site and induce strong cell–cell adhesion. (Lower) Without  $\alpha$ -catenin, cadherin accumulation at the contact site is decreased and the cell–cell adhesion is weakened. (D) Axon–dendrite recognition in hippocampal neurons. Immunostaining for dendrite marker MAP2 of cultured hippocampal neuron and schematic illustrations of dendrite morphology are shown. (Left) Control. (Right) Ectopic expression of nectin-1 to the dendrites. Adapted from [18].

correlate with tissue organization. The expression pattern of each cadherin subclass in embryos correlates with the positional segregation of cell populations. However, there are only a few examples of cadherin-dependent tissue segregation, such as positioning of oocytes during ovary development in the fly, boundary formation between the

cerebral cortex and striatum in the mouse brain, and segregation of motor neurons in the chick spinal cord [8]. Cadherins also contribute to cell segregation by differential expression levels of a single cadherin type. Cells expressing high levels of cadherin sort out from cells expressing low levels of the same cadherin in vitro [9]. During

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