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Receptor-Mediated Endocytosis in Plants

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Abstract Binding of ligands activates cell-surface receptors and triggers a series of signalling events. The activation of the receptors accelerates their internalisation, a process called receptor-mediated endocytosis. Thus, entire receptor–ligand complexes are internalised and processed within the cell. Recent work in a variety of cellular and developmental animal systems further supports the idea that the role of endocytosis extends beyond simply controlling the number of receptors at the cell surface. It has been shown that endocytic transport of the receptor complexes regulates signal transduction and mediates the formation of specialised signalling complexes. Signal transduction events can also modulate specific components of the endocytic machinery. Receptor internalisation in plant cells has recently been demonstrated; however, evidence for receptor-mediated endocytosis in plants is just beginning to emerge. In this review, we highlight the most recent advances in the study of receptor-mediated endocytosis in animals and compare them with what is currently known in plant systems.

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Receptor-Mediated Endocytosis in Animal Cells

Plasma membrane receptors transduce extracellular information to targets inside the cell. In animal cells, receptors activated upon ligand binding are efficiently internalised and sorted in endosomes, either for recycling back to the plasma membrane or for degradation within lysosomes. Internalisation can occur via different routes, e.g. clathrin-mediated, caveolin-dependent, clathrin- and caveolin-independent endocytosis and phagocytosis. Endocytosis delivers receptors first to the early endosomes, a heterogeneous population of membrane compartments with tubulo-vesicular morphology that is located at the cell periphery (Fig. 1a). Receptors can either be recycled to the plasma membrane from the peripheral and perinuclear endosomes, early and late recycling compartments respectively, or they progress to lysosomes where they are degraded. Fusion and movement of the early endosomes causes internalised receptors to redistribute to larger compartments in the perinuclear area. Those compartments often show the characteristic morphology of multivesicular bodies (MVBs)—large membrane compartments that contain small vesicles in their lumen. Internalised receptors can either be recycled back to the plasma membrane or can be retained and accumulated

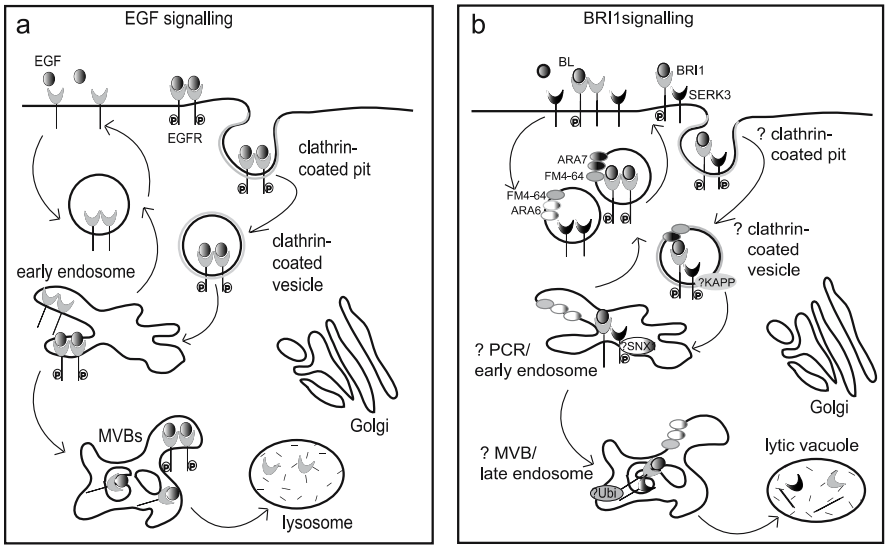

Fig. 1 A comparison of receptor-mediated endocytosis in animal and plant cells. **a** Epidermal growth factor (EGF) receptor is activated by the EGF and endocytosed mainly through clathrin-coated pits. The activated receptor accumulates in early endosomes and multivesicular bodies (MVBs). Ligand-free receptors are almost exclusively recycled to the cell surface. Ligand-bound receptors are sorted to lysosomes for degradation with an increased efficiency compared with that of the ligand-free receptors. EGF receptor remains active in early endosomes and in MVBs, indicated by the presence of phosphate groups. **b** Hypothetical model showing that brassinosteroid receptor complex including BRI1 and AtSERK3 is internalised in FM4-64 positive compartments that are colabelled with Rab5 plant homologues represented by ARA6 or ARA7. Homodimeric combinations of BRI1 and AtSERK3 are internalised and cycle back to the plasma membrane. Heterodimeric combination of BRI1 and AtSERK3 is preferentially internalised for degradation. We propose a general mechanism for degradation of the internalised receptors retained in the early endosomes and MVB compartments that involve KAPP dephosphorylation followed by ubiquitination.

into the MVBs. The multiple invaginations of the MVB membrane serve to trap receptors inside the MVBs, and thus to prevent recycling and to promote their delivery to the lysosomes. In contrast, inactive and ligand-free receptors are almost exclusively recycled back to the cell surface. Ligand-occupied receptors, however, recycle through rapid and slow pathways from early or MVB/late endosomal compartments (reviewed by Sorkin and Zastrow, 2002; Teis and Huber, 2003).

Endocytosis has long been recognised as a means to terminate signalling via degradation of activated receptor complexes after their internalisation from the cell surface. However, it has become clear that the output of the signalling process depends not only on the activation of a particular set of signalling molecules, but also on where or for how long the signal is emitted.