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Endocytosis and Actomyosin Cytoskeleton

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Abstract Mutual interactions between actin and endocytic assembly machineries are essential for successful clathrin-mediated endocytosis in yeast and mammals. The actin cytoskeleton is indispensable for endocytic internalization and for short-range transport of endocytic vesicles. In plants as well, actin seems to be essential for endocytic recycling of plasma membrane proteins and sterols, but surprisingly also for the turnover of cell wall pectins, which have been identified as a major cargo of endocytic vesicles. Endosomes in animal cells perform long-range movements along microtubules, whereas plant endosomes use preferentially an actin polymerization mechanism but also actin tracks for their short- and long-range movements, respectively. Thus, the actin cytoskeleton not only assists endocytic internalization and is in fact inherently associated with endosomal vesicles and endosomes, but also is responsible for their movements at the cell cortex and for their targeted delivery into the cell interior.

1 Introduction

The exact role of the actin cytoskeleton during endocytosis has been a matter of debate during the last decade (reviewed by Engqvist-Goldstein and Drubin, 2003 for yeast and mammalian cells, and by Šamaj et al., 2004 for plant cells). Many possible functions have been proposed (or at least anticipated) for the actin cytoskeleton in various stages of endocytic internalization including an inhibitory effect on vesicle formation, restriction of endocytosis to distinct plasma membrane sites and invagination of plasma membrane, as well as vesicle fission, fusion and motility within the cytoplasm (reviewed by Qualmann et al., 2000; May and Machesky, 2001). It was revealed that actin polymerization and assembly is spatio-temporally coordinated with clathrin-dependent endocytosis, and many endocytic proteins were found to interact with actin-binding proteins putting them in a po-

tentially favourite place to regulate actin dynamics (Engqvist-Goldstein and Drubin, 2003). Nevertheless, a direct functional role for actin during the formation of clathrin-coated vesicles was missing until very recently. Now some evidence has appeared supporting the notion of a functional role played by the actin cytoskeleton during endocytosis (Kaksonen et al., 2003). This new evidence suggests that filamentous actin (F-actin) dynamics is in fact a crucial and indispensable component of the endocytic machinery. Actin patches in yeast were unambiguously identified as sites of endocytic activity and their motility was characterized in more detail (Kaksonen et al., 2003; Huckaba et al., 2004). Moreover, pharmacological disruption of the actin cytoskeleton in mammalian cells with latrunculin and jasplakinolide revealed that F-actin is absolutely required for multiple stages of clathrin-dependent endocytosis including clathrin-coated pit (CCP) formation, constriction and internalization of clathrin-coated vesicles (CCVs), as well as for their lateral mobility, splitting and merging (Yarar et al., 2005). In plants, several pharmacological studies using cytochalasins, latrunculins and jasplakinolide revealed that actin is necessary for endocytic recycling of plasma membrane proteins, sterols and cell wall pectins (Geldner et al., 2001; Baluška et al., 2002; Grebe et al., 2003; Šamaj et al., 2004) and also for fluid-phase endocytosis (Baluška et al., 2004). As far as endocytosis-dependent cytomorphogenesis is concerned, it was shown that tip growth both in pollen tubes and root hairs requires a dynamic actin cytoskeleton (Gibbon et al., 1999; Baluška et al., 2000; Vidali et al., 2001; Šamaj et al., 2002; Staiger et al., 2000; Bloch et al., 2005).

2
Endocytosis and the Actin Cytoskeleton

During the last ten years, numerous studies have revealed that all forms of endocytosis in diverse eukaryotic cells ranging from yeast to plants and mammals require an intact and dynamic actin cytoskeleton, at least in some stages of endocytic internalization (reviewed by Qualmann et al., 2000; May and Machesky, 2001; Engqvist-Goldstein and Drubin, 2003; and Šamaj et al., 2004). Cell biological studies in mammalian cells demonstrated that F-actin is recruited to endocytic sites during internalization in clathrin- and caveolae-mediated endocytosis, as well as in macropinocytosis and phagocytosis. Additionally, diverse endosomes, lysosomes and vesicles use actin comet tails similar to those originally described for the pathogen *Listeria monocytogenes* for their movements via a rocketing mechanism based on localized bursts of actin polymerization (reviewed by Goldberg, 2001; Taunton, 2001; Yarar, 2003; and Engqvist-Goldstein and Drubin, 2003). In *Listeria* comet tails, WASP and ARP2/3 complexes are key components in the regulation of actin polymerization, and the same protein components are also involved