

REVIEW

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Distribution, dynamics and functional roles of phosphatidylserine within the cell

Jason G. Kay^{1*} and Gregory D. Faim^{2,3,4*}

Abstract

Phosphatidylserine (PtdSer), an essential constituent of eukaryotic membranes, is the most abundant anionic phospholipid in the eukaryotic cell accounting for up to 10% of the total cellular lipid. Much of what is known about PtdSer is the role exofacial PtdSer plays in apoptosis and blood clotting. However, PtdSer is generally not externally exposed in healthy cells and plays a vital role in several intracellular signaling pathways, though relatively little is known about the precise subcellular localization, transmembrane topology and intracellular dynamics of PtdSer within the cell. The recent development of new, genetically-encoded probes able to detect phosphatidylserine is leading to a more in-depth understanding of the biology of this phospholipid. This review aims to give an overview of recent developments in our understanding of the role of PtdSer in intracellular signaling events derived from the use of these recently developed methods of phosphatidylserine detection.

Keywords: Phosphatidylserine, Plasma membrane, Flippase, Scramblase

Background

The ability to produce phosphatidylserine (PtdSer) is essential for mammalian survival [1], while the lack of PtdSer production in yeast leads to growth defects and an increase in other negatively charged lipids in an attempt at compensation [2, 3]. In addition, over production of PtdSer leads to the congenital disease Lenz-Majewski syndrome, characterized by the combination of sclerosing bone dysplasia, intellectual disability and distinct craniofacial, dental, cutaneous and distal-limb anomalies [4].

PtdSer has important roles in apoptosis and blood clotting, and most of what is known about PtdSer applies to these roles. However, in homeostasis PtdSer is not generally externally exposed, yet it clearly plays a vital role in healthy cells. The function of PtdSer, as with all lipids, is determined by both its concentration and sidedness in individual organellar membranes. Mitochondria associated membranes (MAMs) of the endoplasmic reticulum (ER) have high rates of PtdSer synthesis and serve as a conduit for the transfer of lipids between the ER and adjacent mitochondria [5, 6]. The bulk subcellular distribution of

PtdSer results from the coordinated actions of metabolic enzymes in conjunction with vesicular and nonvesicular transport pathways, while the topology of PtdSer results from the actions of transmembrane enzymes capable of moving PtdSer between lipid bilayers: PtdSer flippases, floppases, and scramblases [7, 8]. Until relatively recently, PtdSer distribution and topology studies depended solely on the fractionation and subsequent chemical analysis of cellular organelles. These early studies highlighted PtdSer distribution throughout the cell is unbalanced (Fig. 1a), being more concentrated in the plasma membrane (PM) (~ 10–15% total lipid) with lower levels in the ER (~ 4%) and mitochondria (~ 1%), the latter of which uses PtdSer as a source of phosphatidylethanolamine (PtdEtn) (reviewed in [7, 9, 10]). The PtdSer content of less abundant organelles, including the endosomal system, has generally been less well defined because of the difficulty inherent in purifying them to homogeneity.

In addition to difference of PtdSer content amongst organelles, the unequal bilayer distribution of PtdSer at the PM has long been appreciated [11], as has the importance of movement of PtdSer from the cytoplasmic to exofacial face of the PM being involved in critical signaling events including blood clotting [12] and apoptotic cell recognition and removal by macrophages [13]. Furthermore, the PM has a net-negative charge on its

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