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poses the question: are other motors regulated in a similar manner at the point of cargo delivery?

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## Thrilling transcription through threonine phosphorylation

Luciano Di Croce & Ramin Shiekhattar

**Covalent modifications of histone tails are highly correlated with different states of gene expression. Although the biological significance of many such modifications has been elucidated, the physiological role of Thr 11 phosphorylation on histone H3 (H3T11) has remained elusive.**

Steroid hormone receptors are transcription factors that regulate transcription in an exquisite manner<sup>1</sup>. In the absence of ligand, hormone receptors either remain inactive in the cytoplasm or repress promoter activity through the recruitment of co-repressors, including histone deacetylase enzymes (HDACs). Co-repressors are dislodged by ligand binding and hormone receptors then initiate promoter activation through the recruitment of co-activator complexes that possess histone acetyltransferase and chromatin-remodelling activities. Cycles of acetylation and deacetylation at histone tails are among the many dynamic covalent modifications that nucleosomes endure<sup>2</sup>. Phosphorylation, ubiquitination, methylation, sumoylation and ADP-ribosylation also occur on several histone tail residues and are linked closely with the transcriptional activity of many promoters. It has also been suggested that such modifications convey epigenetic information. Steroid hormone receptors have served as a model for the functional interplay between transcription factors and their corresponding chromatin-modifying transcriptional co-activators or co-repressors. Indeed, recent studies have documented the interaction of such receptors with a number of enzymes capable of modifying histone tails in both normal<sup>3</sup> and pathological states<sup>4</sup>.

Many of the histone modifications have been studied in detail; however, very little is known about the biological function of histone H3 Thr 11 (H3T11) phosphorylation. Early studies in plant and mammalian cells suggested that phosphorylation of H3T11 might be involved in chromosome condensation during mitosis and meiosis<sup>5</sup>. On page 53 of this issue, Metzger *et al.*<sup>6</sup> demonstrate that H3T11 phosphorylation is linked to transcriptional regulation in response to stimulation with androgen receptor agonists. The protein-kinase C-related kinase 1 (PRK1) is required for androgen-receptor-dependent gene transcription<sup>7</sup>. Interestingly, the authors show that inhibition of PRK1 (either with the specific inhibitor Ro318220 or by stable RNA interference-mediated silencing) prevents androgen-receptor-mediated H3T11 phosphorylation at the promoter of prostate-specific antigen (PSA). Analysis of the PSA promoter has important implications, as aberrant regulation of PSA has not only been associated with a large number of human prostate tumours but also serves as an early marker for diagnosis of prostate cancer. Metzger *et al.* show that in prostate tumour cells, androgen receptors interact directly with PRK1 and occupy the same region on the PSA promoter. Indeed, the presence of PRK1 is strictly required for H3T11 phosphorylation. In addition, PRK1 is able to phosphorylate H3T11 *in vitro*.

In a previous study, the histone demethylases

in a coordinated fashion<sup>8</sup>. These authors have extended their analyses to show that phosphorylation of H3T11 facilitates Lys 9 (K9) demethylation by the demethylase JMJD2C (Jumonji C (JmjC) domain-containing protein). One interpretation of these results is that trimethylated K9-containing nucleosomes are better substrates for JMJD2C when H3T11 is phosphorylated. Alternatively, PRK1 may phosphorylate JMJD2C directly to enhance its demethylation activity. As H3K9 trimethylation (a docking site for an important component of heterochromatin, heterochromatin protein 1 (HP1; refs 9, 10)) has been correlated closely with transcriptional repression, reduced levels of trimethyl K9 caused by H3T11 phosphorylation may lead to transcriptional activation.

Enhancement of H3K9 demethylation accounts for only part of the effects of PRK1/H3T11 phosphorylation in regulating promoter activity. Metzger *et al.* provide additional data correlating PRK1 occupancy at target promoters with the activation of the transcription complex from a pre-initiation to an initiation state, as measured by phosphorylation of the RNA polymerase II at Ser 5. Impairment of PRK1 activity prevents Ser 5 phosphorylation but not the recruitment of RNA polymerase II to the promoter, suggesting a provocative crosstalk between H3T11 phosphorylation, H3K9 demethylation and the critical switch from a pre-initiation to initiation complex.

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