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Histone acetylation and chromatin remodeling: which comes first?

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1. Introduction

The packaging of DNA into chromatin prevents access of the transcription machinery necessary to regulate gene expression. To overcome this repressive barrier, the cell contains numerous, multi-subunit chromatin-remodeling enzymes, which work to loosen and open up chromatin structure. The SWI/SNF complex is a multi-subunit, ATP-dependent chromatin-remodeling machine. It is able to use the energy of ATP hydrolysis to alter histone-DNA contacts, and in many cases, leads to movement of the histone octamer along DNA or to transfer of the octamer to another chromosome (for reviews, see [1,2]). The SAGA complex represents a second class of chromatin-remodeling complexes, histone acetyltransferases (HATs), which covalently modify the amino terminal tails of the histone proteins, possibly leading to alteration of histone-DNA or histone-histone interactions. The multi-subunit SAGA complex contains the yeast Gcn5 protein that possesses its catalytic activity, and has many components that were previously described as being involved in transcription regulation, including Ada, Spt, and Taf proteins (for review, see [3]).

2. Evidence for functional interplay between SWI/SNF and SAGA

Over the last few years, evidence for a functional interaction between SWI/SNF and HAT complexes, and in particular the SAGA complex, has accumulated.

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Many inducible genes whose expression is dependent on the yeast SWI/SNF complex also have been found to be dependent on Gcn5. These genes include *INO1*, *HO*, *SUC2*, *HIS3*, and Ty elements [4–8]. Moreover, *GCN5* and genes encoding SWI/SNF components exhibit similar genetic interactions with chromatin components. Mutations in the *SIN1* gene, which likely encodes a nonhistone component of chromatin and a distant relative of mammalian HMG1, partially alleviates transcriptional defects caused by inactivation of the SWI/SNF complex as well as disruption of GCN5/ADA-containing HAT complexes (*ada2sin1* and *ada3sin1* double mutants were tested) [5,9,10]. Also, similar to mutations in *SIN1*, semidominant mutations (*sin* alleles) in *HHT2* (gene encoding histone H3) and *HHF2* (gene encoding histone H4) were able to partially alleviate transcriptional defects due to inactivation of SWI/SNF and loss of GCN5 [5,11]. SWI/SNF components and SAGA components have been shown to be synthetically sick, or in some cases, synthetically lethal, with each other, indicating that they may play partially redundant or overlapping roles in the cell. In particular, Spt20, a component of SAGA, was shown to be synthetically lethal with Swi2/Snf2, Snf5, and Swi1 [6]. Furthermore, another Spt family member and component of SAGA, Spt7 was also synthetically lethal with Swi2/Snf2. Also, Gcn5, Ada2, and Ada3 were each found to be either synthetically sick or lethal with Swi2/Snf2, Snf5, or Swi1 [5,6]. These phenotypes suggest that the two types of complexes perform overlapping functions related to the transcription of genes necessary for proper cell growth and survival. It is also possible that the complexes work in parallel pathways and the cell dies when both are lost. Alternatively, the complexes may be interacting functionally and work most effectively when in the presence of each other.

Both the SWI/SNF and SAGA complexes have been shown to directly interact with a similar set of

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