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## The Structure of the Follistatin:Activin Complex Reveals Antagonism of Both Type I and Type II Receptor Binding

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### Summary

TGF- $\beta$  ligands stimulate diverse cellular differentiation and growth responses by signaling through type I and II receptors. Ligand antagonists, such as follistatin, block signaling and are essential regulators of physiological responses. Here we report the structure of activin A, a TGF- $\beta$  ligand, bound to the high-affinity antagonist follistatin. Two follistatin molecules encircle activin, neutralizing the ligand by burying one-third of its residues and its receptor binding sites. Previous studies have suggested that type I receptor binding would not be blocked by follistatin, but the crystal structure reveals that the follistatin N-terminal domain has an unexpected fold that mimics a universal type I receptor motif and occupies this receptor binding site. The formation of

follistatin:BMP:type I receptor complexes can be explained by the stoichiometric and geometric arrangement of the activin:follistatin complex. The mode of ligand binding by follistatin has important implications for its ability to neutralize homo- and heterodimeric ligands of this growth factor family.



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