experiments containing GroES yielded very similar data (Fig. 3*d*). Thus, β-actin released from GroEL is recognized and cycled by c-cpn at least as efficiently as β-actin diluted from denaturant. Similar data were obtained using α-tubulin as target protein (Fig. 3*e*, *f*). We conclude that GroEL can form a binary complex with labelled unfolded β-actin or α-tubulin and releases them in an ATP-dependent manner, but cannot aid their proper folding, with or without GroES.

We also found that mt-cpn, like GroEL, cannot help the productive folding of β-actin or α-tubulin (data not shown); however, mt-cpn can cycle these target proteins (although to different extents compared with GroEL) (Fig. 3*g*–*j*). We conclude that actin and tubulin target proteins can both be discharged from GroEL or mt-cpn in the presence of ATP in a spectrum of states that, though recognizable by c-cpn, cannot proceed directly to the native state. Rather, they are confined to an endless cycle of binding to and release from different GroEL or mt-cpn molecules.

To look for differences in the state of chaperonin-bound target proteins, we compared their sensitivity to two different proteases (Fig. 4). In the absence of ATP, β-actin bound to GroEL, mt-cpn or c-cpn has a similar low resistance to protease, suggesting that the three chaperonins have the same ability to unfold proteins. However, protease-resistant states do accumulate when β-actin is cycled by GroEL in the presence of GroES (Fig. 4*f*). The protease sensitivity of β-actin cycled by c-cpn cannot be interpreted because of the accumulation of protease-resistant native product, but when α- or β-tubulin is cycled by c-cpn, protease-resistant states are generated (G.T. *et al.*, manuscript in preparation). Thus, c-cpn and GroEL/GroES produce more native-like spectra of folding intermediates than either GroEL alone or mt-cpn, with or without cpn10.

It has been proposed that chaperonins function by unfolding kinetically trapped intermediates[7,8]. However, they do not function in a manner that mimics unfolding by urea or guanidine, because all three chaperonins can aid the folding of target proteins (even following a single round of interaction) under conditions in which no spontaneous folding would occur upon dilution from denaturant. These considerations and the data presented here imply that a distinct set of folding intermediates is released from different chaperonins. Our data suggest that chaperonin-bound actin or tubulin target proteins are extensively unfolded; however, when cycled by GroEL/GroES, and even more so when cycled by c-cpn, significant higher order structure is acquired. Thus, GroEL, mt-cpn and c-cpn seem to differ not in their ability to unfold or cycle proteins, but in their ability to generate productive folding intermediates. □

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## ERRATUM

# Glycogen synthase kinase-3 and dorsoventral patterning in *Xenopus* embryos

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IN the legends to Figs 2*d* and 3*b* of this Article, the shading of histogram bars was incorrectly designated. These should be: white bar, normal embryo; hatched bar, incomplete axis duplication; black bar, complete axis duplication. □

## CORRECTIONS

# XLαs is a new type of G protein

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WE wish to report a discrepancy in the predicted size of XLαs and its apparent size on SDS–PAGE. To express XLαs, we transfected PC12 cells with a composite clone assembled from clones CDM8-XL, RACE I.24 and RACE II.7 (see Methods in Fig. 2*c* legend) which contains the open reading frame that runs from the ATG at nucleotides 46–48 to the CTC at nucleotides 2,581–2,583 (Fig. 2*c*). Surprisingly, this composite clone, which encodes a polypeptide of relative molecular mass 92K, yields a protein with an apparent mobility of 124K on SDS–PAGE. Expression in PC12 and CHO cells of the clone CDM8-XL (nucleotides 380–2,956; Fig. 2*c*), which encodes a polypeptide of relative molecular mass 78K, yields a protein with an apparent electrophoretic mobility of 94K, identical to the endogenous XLαs of PC12 cells. Thus it appears that translation of XLαs starts at the ATG at nucleotides 439–441, resulting in a 715-amino-acid protein of relative molecular mass 78K (XL portion, 367 amino acids; relative molecular mass 37K) with an anomalous electrophoretic mobility. This does not affect any of the conclusions of our study, except that the N-terminal domain preceding the EPAA repeats (Fig. 2*c*, *d*) is shorter than we assumed. The significance of the open reading frame starting at the ATG at nucleotides 46–48 remains to be investigated. □

# An Early Miocene anthropoid skull from the Chilean Andes

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THE captions of parts *b* and *c* of Fig. 1 legend in this Letter were transposed as published. □