kinesin-14 family members? In the case of NCD, *in vivo* observations have not revealed a role for depolymerase activity. NCD is required for spindle assembly and maintenance of bipolarity in the *Drosophila* early embryo, and chromosome segregation in meiosis [16,18]. It is not clear at this time how these activities might be linked to plus end depolymerase activity, however minus end directed motility has been implemented in these functions. Testing the role of NCD depolymerase *in vivo* will likely prove challenging due to the complex nature of the mitotic spindle. Nevertheless, similar studies on other kinesin-14 proteins will help shed light on the biological mechanism of this interesting protein family.

Given our extensive knowledge of Kar3p function during mating, what can we say about its mechanistic role during mitosis? Recently, Tanaka *et al.* [19] showed that, in mitosis, the minus end directed motor activity of Kar3p contributes to bi-orientation of chromosomes on the spindle. This study did not, however, present specific observations that are consistent with plus end depolymerase activity for Kar3p in the mitotic spindle. Interestingly, Kar3p in the nucleus is thought to interact with a different light chain (Vik1p) than that in the cytoplasm (Cik1p [20]). It is possible that differential light chain binding can bias Kar3p toward either motility (Vik1p) or depolymerase activity (Cik1).

Future studies on the depolymerase activity of Kar3p/Vik1p complex should yield interesting results and help to better understand this important motor molecule. In any case, this fascinating bi-functional motor protein will continue to provide insight into the ubiquitous problem of microtubule based force production throughout biology.

References

1. Sproul, L.R., Anderson, D.J., Mackey, A.T., Saunders, W.S., and Gilbert. S.P. (2005). Cik1 targets the minus-end kinesin depolymerase Kar3 to microtubule plus-ends. Curr. Biol. 15, 1420–1427.
2. Meluh, P.B., and Rose, M.D. (1990). KAR3, a kinesin-related gene required for yeast nuclear fusion. Cell *60*, 1029–1041.
3. Marsh, L., and Rose, M. The Pathway of Cell and Nuclear Fusion during Mating in S. cerevisiae. In *The Molecular and Cellular Biology of the Yeast Saccharomyces*, ed. J.R. Pringle, J.R. Broach, and E.W. Jones. Vol. 3. 1997, Cold Spring Harbor Laboratory Press: Cold Spring Harbor. 827-888.
4. Maddox, P.S., Bloom, K.S., and Salmon, E.D. (2000). The polarity and dynamics of microtubule assembly in the budding yeast Saccharomyces cerevisiae. Nat. Cell Biol. *2*, 36–41.
5. Maddox, P., Chin, E., Mallavarapu, A., Yeh, E., Salmon, E.D., and Bloom, K. (1999). Microtubule dynamics from mating through the first zygotic division in the budding yeast Saccharomyces cerevisiae. J. Cell Biol. *144*, 977–987.
6. Cleveland, D.W., Mao, Y., and Sullivan, K.F. (2003). Centromeres and kinetochores: from epigenetics to mitotic checkpoint signaling. Cell *112*, 407–421.
7. Maddox, P.S., Stemple, J.K., Satterwhite, L., Salmon, E.D., and Bloom, K. (2003). The minus end-directed motor Kar3 is required for coupling dynamic microtubule plus ends to the cortical shmoo tip in budding yeast. Curr. Biol. *13*, 1423–1428.
8. Endow, S.A., Kang, S.J., Satterwhite, L.L., Rose, M.D., Skeen, V.P., and Salmon, E.D. (1994). Yeast Kar3 is a minus-end microtubule motor protein that destabilizes microtubules preferentially at the minus ends. EMBO J. *13*, 2708–2713.
9. Saunders, W., Hornack, D., Lengyel, V., and Deng, C. (1997). The Saccharomyces cerevisiae Kinesin-related motor Kar3p acts at preanaphase spindle poles to limit the number and length of cytoplasmic microtubules. J. Cell Biol. *137*, 417–432.
10. Huyett, A., Kahana, J., Silver, P., Zeng, X., and Saunders, W.S. (1998). The Kar3p and Kip2p motors function antagonistically at the spindle poles to influence cytoplasmic microtubule numbers. J. Cell Sci. *111*, 295–301.
11. Page, B.D., Satterwhite, L.L., Rose, M.D., and Snyder, M. (1994). Localization of the Kar3 kinesin heavy chain-related protein requires the Cik1 interacting protein. J. Cell Biol. *124*, 507–519.
12. Walczak, C.E. (2003). The Kin I kinesins are microtubule end-stimulated ATPases. Mol. Cell *11*, 286–288.
13. Hunter, A.W., Caplow, M., Coy, D.L., Hancock, W.O., Diez, S., Wordeman, L., and Howard, J. (2003). The kinesin-related protein MCAK is a microtubule depolymerase that forms an ATP-hydrolyzing complex at microtubule ends. Mol. Cell *11*, 445–457.
14. Moores, C.A., Yu, M., Guo, J., Beraud, C., Sakowicz, R., and Milligan, R.A. (2002). A mechanism for microtubule depolymerization by KinI kinesins. Mol. Cell *9*, 903–909.
15. Niederstrasser, H., Salehi-Had, H., Gan, E.C., Walczak, C., and Nogales, E. (2002). XKCM1 acts on a single protofilament and requires the C terminus of tubulin. J. Mol. Biol. *316*, 817–828.
16. Endow, S.A., Henikoff, S., and Soler-Niedziela, L. (1990). Mediation of meiotic and early mitotic chromosome segregation in Drosophila by a protein related to kinesin. Nature *345*, 81–83.
17. Walker, R.A., Salmon, E.D., and Endow, S.A. (1990). The Drosophila claret segregation protein is a minus-end directed motor molecule. Nature *347*, 780–782.
18. Sharp, D.J., Brown, H.M., Kwon, M., Rogers, G.C., Holland, G., and Scholey, J.M. (2000). Functional coordination of three mitotic motors in Drosophila embryos. Mol. Biol. Cell *11*, 241–253.
19. Tanaka, K., Mukae, N., Dewar, H., van Breugel, M., James, E.K., Prescott, A.R., Antony, C., and Tanaka, T.U. (2005). Molecular mechanisms of kinetochore capture by spindle microtubules. Nature *434*, 987–994.
20. Manning, B.D., Barrett, J.G., Wallace, J.A., Granok, H., and Snyder, M. (1999). Differential regulation of the Kar3p kinesin-related protein by two associated proteins, Cik1p and Vik1p. J. Cell Biol. *144*, 1219–1233.

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Brain Evolution: Getting Better All the Time?

Recent studies on bats, goats and hominids suggest that some mammalian brains may have undergone dramatic evolutionary reductions in size. These studies emphasise the importance of selective pressures upon mammalian brain evolution and the need to integrate studies of neuroanatomy, neurophysiology and behaviour.

Jeremy E. Niven

Animals possess traits that convey a selective advantage but which are often costly in terms of energy and resources, resulting in a trade-off between costs and benefits [1]. Changes in the ecology or behaviour of the animal may reduce the selective advantage of a particular trait, potentially leading to its reduction or loss. Vision, for example, is vital for predator and prey detection, conspecific recognition and navigation, but in low light environments such as caves it has frequently been lost. The brain is subject to the same selective pressures as other traits. Therefore, when energy and resources are limiting and demands on neural processing are reduced, brains would be expected to get smaller. Indeed, the exceptionally high energetic cost of the brain suggests that it would be under strong pressure to reduce cost.

There is certainly evidence to support the reduction of specific brain regions such as the visual systems of cave fish. Examples of brain size reduction under domestication also exist [2] and, although this is artificial selection, they clearly show that such changes are possible. Yet reduction in brain size has received little attention during over 100 years of comparative brain analysis in vertebrates [3,4]. Most studies of the vertebrate brain have focussed exclusively upon expansion of the brain or specific brain regions [5–8], emphasising their expansion in relation to behavioural specializations [7,8]. For example, the degree of specialization for food hoarding in birds is highly correlated with the relative size of their hippocampus [7], whilst neocortical volume in primates is correlated with deception rate [8].

Three recent studies [9–11] show that brain size reduction may have occurred in several mammalian lineages under different conditions. These studies show the reduction of brain mass relative to the body mass, an important consideration as brain mass scales allometrically making absolute brain size a potentially misleading measure. The first study documents brain size reduction in an extinct bovid genus, *Myotragus* [9]. *Myotragus* fossils are found on two islands, Majorca and Menorca, and are related to the chamois goat (*Rupicapra rupicapra*). Having crossed from the mainland to these islands during a drop in sea level, *Myotragus* was subsequently isolated and underwent a substantial reduction in brain mass: 50% compared to living bovids of similar body mass. To be certain *Myotragus* underwent brain size reduction, however, it is essential to know the brain size of its continental ancestor; the primary candidate is another fossil bovid, *Gallogoral meneghini*, whose relative brain mass is similar to that of other fossil and living bovids, confirming the dramatic brain size reduction in *Myotragus* [9].

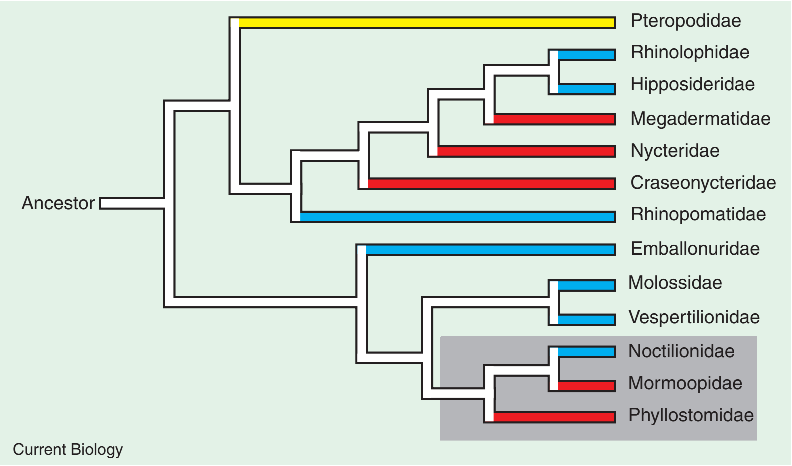

Figure 1. A phylogenetic tree of Chiropteran families showing changes in relative brain mass.

Branches containing some species showing brain size reduction in blue, expansion in red and a mixture in yellow. All families contain some species possessing the ancestral brain size. Lineages that evolved in Gondwana are highlighted by a grey box. (Data: Kamran Safi, Zoologisches Institut, Universität Zürich).

What factors led to the reduction of *Myotragus's* brain? One key factor is likely to be the isolation of *Myotragus* on an island. Islands often have a depleted fauna compared to the mainland and Majorca lacked large mammalian predators. The impoverishment of the island ecosystem and the release from predation pressure may have reduced the requirement for *Myotragus* to support a large brain. Resource limitation may also have played an important role. Foraging opportunities are often limited on islands and, in the absence of predation, *Myotragus* populations may have expanded, increasing pressure on energetic expenditure.

Is brain size reduction limited to islands? A second study on bats suggests that it may be far more wide-ranging [10]. Reconstruction of the ancestor of modern bats suggests that it had intermediate wing area, body mass and brain mass, implying that some modern bat species may have undergone brain size reduction whilst others have expanded their brains [10]. Brain size reduction seems to have occurred in some species of at least eight families, whilst expansion occurred in six families (Figure 1). Both reduction and expansion are evident in families thought to have evolved independently on Laurasia and Gondwana, suggesting independent reduction of relative brain size (Figure 1).

One explanation for brain size reduction in bats could be their foraging strategies and habitiat complexity [10,12]. Habitat complexity correlates with relative brain size for animal-eating bats but not for plant-eating bats, which all tend to have relatively large brains, suggesting that habitat and foraging strategy affect brain size [10]. Bats with smaller brains hunt in open, uncluttered environments, which presumably place lower demands on neural processing whilst those with larger brains hunt in cluttered, complex environments requiring high levels of neural processing. Energetic constraints are also an important consideration for flying animals. Excessively large brains not only consume energy but also require large amounts of energy to carry. Therefore, as in *Myotragus*, brain reduction has occurred when demands on neural processing are reduced and energy is limiting.

The recent discovery of a small-brained fossil hominid, *Homo floresiensis*, on the island of Flores in Indonesia [11,13] raises many important questions about brain size [14]. Although the brain of *H.*

floresiensis is smaller in absolute terms than that of its putative ancestor, *H. erectus*, the reduction in relative brain size may be small depending upon the exact body mass estimate. *H. floresiensis* has a brain 2.5–4.6 times larger than expected for an ‘average’ mammal of equivalent body mass, whereas the value for *H. erectus* is 3.3–4.4 times, suggesting that their relative brain size may been similar [11]. Any brain size reduction that has occurred may have been due to the same factors as in *Myotragus* and the Chiroptera: reduced demands on neural processing and an increased pressure on energetic expenditure. If reduction has occurred, this suggests that *H. floresiensis* may not have been capable of the behavioural complexity observed in modern humans. However, archaeological evidence found near *H. floresiensis* suggests it was capable of tool use and of possibly harnessing fire [15].

The discovery of *H. floresiensis* emphasises that the relationship between brain size and behavioural complexity remains unclear. Brain size affects the number of neurons in the brain and, therefore, the number and complexity of possible neural circuits. Increased numbers of neurons enable better sensory processing and motor control, but may also be linked to behavioural complexity (for example [7,8]). However, absolute brain size does not appear to be as important as relative brain size in determining behavioural complexity, because whales and elephants have larger brains than humans [4]. Relative brain size appears to be linked to resting metabolic rate [16]. Energy places limits on both the total numbers of neurons — because of maintenance costs — and the density of neural activity. Calculations suggest that in both the rat and the human brains only a small proportion of neurons are active at any particular time, because of the high energetic costs of neural signalling [17,18]. One possibility is that, although larger animals have greater numbers of neurons, their brains also have lower mass specific metabolic rates, suggesting lower densities of neural activity at any particular time. The relative reduction or expansion of brains would alter the number of neurons and neural circuits but not the density of neural activity, producing fewer or more neurons active simultaneously. Therefore, the relationships between numbers of neurons, their activity and their energy consumption may be key to understanding links between relative brain size and behavioural complexity. Studies on *Myotragus*, bats and *H. floresienses* demonstrate the potential effects of selective pressures on relative brain size. To understand the implications of changes in relative brain size, however, neurophysiology and behaviour are also essential.

References

1. Darwin, C.R. (1859). On the Origin of Species. (London: John Murray).
2. Kruska, D.C.T. (2005). On the evolutionary significance of encephalization in some eutherian mammals: effects of adaptive radiation, domestication and feralization. Brain Behav. Evol. *65*, 73–108.
3. Jerison, H.J. (1973). Evolution of the Brain and Intelligence. (New York: Academic Press)
4. Striedter, G.F. (2005). Brain Evolution. (Sunderland: Sinauer Associates Inc. US)
5. Barton, R.A., and Harvey, P.H. (2000). Mosaic evolution of brain structure in mammals. Nature *405*, 1055–1058.
6. Harvey, P.H., and Krebs, J.R. (1990). Comparing brains. Science *249*, 140–146.
7. Lucas, J.R., Brodin, A., de Kort, S.R., and Clayton, N.S. (2004). Does hippocampal size correlate with the degree of caching specialization? Proc. Biol. Sci. *271*, 2423–2429.
8. Byrne, R.W., and Corp, N. (2004). Neocortex size predicts deception rate in primates. Proc. Biol. Sci. *271*, 1693–1699.
9. Köhler, M., and Moyá-Solá, S. (2004). Reduction of brain and sense organs in the fossil insular bovid *Myotragus.* Brain Behav. Evol. *63*, 125–140.
10. Safi, K., Seid, M., and Dechmann, D.K.N. (2005). Bigger is not always better: when brains get smaller. Biol. Lett. doi: 10.1098/rsbl.2005.0333.
11. Brown, P., Sutikna, T., Morwood, M.J., Soejono, R.P., Jatmiko, Saptomo E.W and Due, R.A (2004). A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. Nature *431*, 1055–1061.
12. Hutcheon, J.M., Kirsch, J.A.W., and Garland, T. (2002). A comparative analysis of brain size in relation to foraging ecology and phylogeny in the Chiroptera. Brain Behav. Evol. *60*, 165–180.
13. Falk, D., Hildebolt, C., Smith, K., Morwood, M.J., Sutikna, T., Brown, P., Jatmiko, Saptomo E.W, Brunsden, B., and Prior, F. (2005). The brain of LB1, *Homo floresiensis*. Science *308*, 242–245.
14. Mirazón Lahr, M., and Foley, R. (2004). Human evolution writ small. Nature *431*, 1043–1044.
15. Morwood, M.J., Soejono, R.P., Roberts, R.G., Sutikna, T., Turney, C.S., Westaway, K.E., Rink, W.J., Zhao, J.-x., van den Bergh, G.D., Due, R.A. *et al.* (2004). Archaeology and age of a new hominin from Flores in eastern Indonesia. Nature *431*, 1087–1091.
16. Martin, R.D. (1981). Relative brain size and basal metabolic rate in terrestrial vertebrates. Nature *293*, 57–60.
17. Attwell, D. and Laughlin, S. (2001). An energy budget for signalling in the grey matter of the brain. J. Cereb. Blood Flow Metab. *21*, 1133–1145.
18. Lennie, P. (2003). The cost of cortical computation. Curr. Biol. *13*, 493–497.

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Sexual Selection: Copycat Mating in Birds

Female zebra finches may be influenced by the choices of other females when selecting mates, challenging the view that mate-choice copying should not occur in species with biparental care.

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Choosing a mate is not a simple business. A female needs a male in order to reproduce, but how does she know which one to pick? How can she find a good mate without wasting too much time and effort? One answer is to watch what other females are doing and choose the same males, or same kind of males, as they do.

For species in which males do not help care for their young, such mate-choice copying might work very well. Females want the healthiest, most attractive males, and the behaviour of other females might guide them to these males. However, if males help to care for their young and females are searching for a good