in asynchronous muscles are achieved by elaboration of stretch activation/release inactivation in muscles that basically have twitches of long duration[12,13].

Synchronous and asynchronous muscles can be distinguished by their fine structure, as Smith[1] points out; the former possess an extensive sarcoplasmic reticulum and T-system and tend to have small myofibrils, whereas the latter tend to have a very reduced sarcoplasmic reticulum and large myofibrils. In cicadas, twitch duration in synchronous tymbal muscles is inversely related to the quantity of sarcoplasmic reticulum within each muscle fibre (R.K.J. and D.Y., in preparation). The faster tymbal muscles also have smaller myofibrils, with myofibril cross-sectional area being the best morphological predictor of twitch duration (Fig. 1*b*). The asynchronous muscle of *P. capitata* is quite different from fast, synchronous muscle (for example, that of *P. claripennis*) in having a large fibril area and in being sparsely supplied with sarcoplasmic reticulum[11].

Thus, synchronous tymbal muscles constitute a graded series, throughout which contraction kinetics and fine structure are closely correlated with the normal operating frequency. We have demonstrated that contraction frequencies of over 200 Hz are achieved within the synchronous mode of operation. Clearly, 100 Hz is not the upper limit of contraction frequency in synchronous muscles.

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1. Smith, D. S. *Nature* **303**, 539–540 (1983).
2. Wootton, R. J. & Newman, D. J. S. *Nature* **280**, 402–403 (1979).
3. Revel, J. P. *J. Cell. Biol.* **12**, 571–588 (1962).
4. Suthers, R. A. & Fattu, J. M. *Am. Zool.* **13**, 1215–1226 (1973).
5. Skoglund, C. F. *J. Biophys. biochem. Cytol.* **10** (Suppl.), 187–200 (1961).
6. Cohen, M. J. & Winn, H. E. *J. exp. Zool.* **165**, 335–370 (1967).
7. Mendelson, M. *J. Cell Biol.* **42**, 548–563 (1969).
8. Josephson, R. K. & Halverson, R. C. *Biol. Bull.* **141**, 411–433 (1971).
9. Josephson, R. K. *J. exp. Biol.* **59**, 781–801 (1973).
10. Young, D. & Josephson, R. K. *J. comp. Physiol.* **152**, 183–195 (1983).
11. Josephson, R. K. & Young, D. *J. exp. Biol.* **91**, 219–237 (1981).
12. Pringle, J. W. S. *Proc. R. Soc.* **B201**, 107–130 (1979).
13. Pringle, J. W. S. *J. exp. Biol.* **94**, 1–14 (1981).

Encephalization in *Proconsul africanus*

WALKER *et al.*[1] recently suggested that the Miocene hominoid *Proconsul africanus* was more encephalized than extant monkeys of similar body size, and they suspected that it may resemble pongids in relative brain size. As an index of encephalization they used an encephalization quotient (EQ) based on a particular allometric equation[2]. Here I re-examine the degree of encephalization of *P. africanus* by applying two additional, but different, indices of encephalization traditionally used in brain–body size studies: one based on the constant of cephalization (CC)[3–5], the other on the extra neurone index (N_c)[6]. Both approaches yield the same result, which is in conflict with that of Walker *et al.* According to these methods, the degree of encephalization of *P. africanus* is within the range of extant monkeys and substantially below that of the apes.

Table 1 Encephalization indices in *Proconsul africanus* and extant apes and monkeys

	EQ	CC	N_c ($\times 10^9$ neurones)
Proconsul africanus	48.8	19.6	1.9
Pan troglodytes	41.1	35.6	3.6
Pongo pygmaeus	31.6	30.1	3.3
Gorilla gorilla	17.2	31.2	3.5
Cercopithecoidea	22.9–82.0	8.0–20.2	0.9–2.1

EQ = brain weight (g)/0.0991 (body weight, g)$^{0.76237}$; CC = brain weight (g)/(body weight, g)$^{0.23}$; for calculation of N_c, see ref. 6.

The equation used by Walker *et al.* provides an excellent fit for brain–body size relationships in high-level taxa such as the class Mammalia (mouse–elephant curve) or the order Primates (mouse lemur–gorilla curve). Because of its high exponent of allometry (0.76), however, it tends to overestimate the degree of encephalization for small-sized species while underestimating encephalization in larger species, when comparisons are made at a lower level of the hierarchy. This is the case because among closely related species or genera, brain weight scales at a much lower power of body weight with values of the exponent of allometry characteristically falling between 0.2 and 0.3 (refs 3, 4, 7, 8). In the study by Walker *et al.* this phenomenon leads to obviously erroneous results such as gorillas being less encephalized than the least encephalized monkey and the range for monkeys surpassing that of the apes at the upper end by a considerable margin (Table 1). Being aware of the strong limitations of their method, Walker *et al.* resort to a comparison of *P. africanus* with similar sized monkeys. While this alleviates the problem somewhat, the fact that the comparison of EQs is based on an equation fitting high-level taxa still leaves a major source of error.

Using the same brain–body size data but an equation based on an exponent of allometry (0.23) consistent with brain–body size relationships among low-level taxa, yields not only different but much more consistent results (Table 1). The CC values for the apes are closely grouped together and substantially above the range for monkeys. *P. africanus* lies towards the upper end of the monkey range. For *P. africanus* to be at the bottom of the range of apes (CC = 30) would require a cranial capacity of 255 cm^3, almost 90 cm^3 larger than the actual estimate, at a body weight estimate of 11 kg. Use of the extra neurone index yields the same results (Table 1): apes fall closely together and are clearly above the monkey range with *P. africanus* in the upper end of the latter.

Thus, while *P. africanus* may share several derived traits with extant apes, relative brain size does not seem to be one of them.

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1. Walker, A., Falk, D., Smith, R. & Pickford, M. *Nature* **305**, 525–527 (1983).
2. Holloway, R. L. & Post, D. G. in *Primate Brain Evolution* (eds Armstrong, E. & Falk, D.) 57–76 (Plenum, New York, 1982).
3. Hemmer, H. *Proc. 3rd int. Congr. Primatol.* (eds Biegert, J. & Leutenegger, W.) 99–107 (Karger, Basel, 1971).
4. Leutenegger, W. *Folia Primatol.* **19**, 9–17 (1973).
5. McHenry, H. M. *Nature* **254**, 686–688 (1975).
6. Jerison, H. *J. Hum. Biol.* **35**, 263–291 (1963).
7. Röhrs, M. *Z. wiss. Zool.* **162**, 1–95 (1959).
8. Gould, S. J. *Contr. Primatol.* **5**, 244–292 (1975).

SMITH AND WALKER REPLY—Leutenegger's discussion and data are a useful addition to the interpretation of relative brain size in *Proconsul africanus*, but careful evaluation of his data confirms our conclusion that *P. africanus* shows a tendency towards the increased encephalization that characterizes apes in comparison with monkeys. The indices used by Leutenegger do not eliminate the confounding effect of size that he correctly noted exists for the values that we reported when using a slope of 0.76 to calculate encephalization quotients.

While our measurement of relative brain size involved an inverse bias—animals with larger body weights having lower EQs—both indices used by Leutenegger show the opposite bias—larger animals having larger values. He reports Hemmer's[1] values for the constant of cephalization (CC) as being in the range 8.0–20.2 for Cercopithecoidea. The value of 8.0 is for the smallest cercopithecoid, *Miopithecus talapoin*, and the largest