mantle itself, or by the new strand of siphuncular cord^{1,7}. Because of the imprecision of air-weighing, however, such weight changes would only be detectable in *Nautilus* producing chambers of ~10 cm³ volume or more, and only in conditions of known and constant weight change due to feeding. Even in controlled aquarium conditions, attaining the latter is difficult, and as seen from Fig. 1, many weight changes of similar magnitude occurred between septal formation events, while some actual formation events did not show this trend. Identifying chamber formation events solely on the basis of weight change patterns, without the benefit of radiography, would be highly inaccurate. Nevertheless, just such evidence has been used to derive rates of chamber formation in *Nautilus*⁸.

The chamber formation cycle in *Nautilus* can thus be viewed as a highly organized and regular process. The shell aperture and the soft parts are constantly growing forward; the septal mantle, however, remains fixed against the various septa for over 90% of the animal's life. It only moves forward when the last formed septum is completely calcified; full calcification coincides with the chamber being half emptied of liquid. The septal mantle is then pulled forward by muscular action, leaving behind a liquid filled space that will become the cameral liquid

of the next chamber. It reattaches and begins secreting a new calcareous septum, that in turn will be abandoned when completely thickened. The osmotically-induced removal of liquid from the chambers occurs at a rate that balances density increases of growing shell and tissue.

Although the period between chamber formation events could be as small as 30 days or less for the low-volume, early chambers produced by very young *Nautilus*, our observations suggest that chamber formation takes very much longer than a month during most of an animal's ontogenetic development. The four *Nautilus* maintained in this study were raised in conditions very different from their native habitat, perhaps resulting in growth rates very different from those in nature. The apertural growth rates ranged between 0.15 and 0.25 mm day⁻¹, values which are comparable with growth rates of similarly sized *N. macromphalus* grown in aquaria^{2,6}.

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Lucy's lower limbs: long enough for Lucy to be fully bipedal?

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The recent attempt to show that the Hadar australopithecine female 'Lucy' (AL 288-1) had hindlimbs too short to allow a modern pattern of striding bipedal gait¹ has important implications for understanding the origin of bipedalism, if not for the more general problem of hominid origins. Combined with previous claims that Lucy had a forelimb unusually long in proportion² and ape-like in morphology³, the additional contention of a relatively short hindlimb would suggest a very different pattern of gait from the norm of today because the effectiveness of the pendulum action of the lower limb during stride is a function of the amount of mass in the limb⁴, and because a short hindlimb would necessitate a short stride length¹. Yet, these contentions seem contradicted by the analyses of Lucy's pelvis (and the innominates of other australopithecines)^{4,5} that indicate a similar pattern of muscle use and imply a lack of significant gait differences. Are Lucy's legs too short to allow an effective stride, or is there a different solution to this contradiction? I propose here that there is.

Jungers¹ attempts to answer the question of whether the high humeral/femoral index of AL 288-1 reflects a relatively long forelimb or a relatively short hindlimb, by expressing each limb length as a deviation from the allometric relation of the limb length to body weight in the African apes. These deviations are compared with deviations for skeletal measures of a pygmy chimpanzee of known weight, an Mbuti Pygmy (MMC-18) of estimated weight and a European sample of known weight. The results show a femoral deviation for Lucy like that of the chimpanzee and much less than that of the human, but a humeral deviation like the human's and in the opposite direction to the chimpanzee, leading to the conclusion that the evidence does not support an interpretation of "a fully modern adaptation to bipedalism". I contend that this conclusion comes from a misinterpretation of the data, and that the hindlimb of

AL 288-1 is the length one would expect in a hominid of her size.

Part of the problem comes from the Mbuti Pygmy weight used, as it is actually no more than a guess⁶; the maximum estimate of 30.9 kg is the average weight (*Wt*) for a 12-yr old Pygmy female⁷. To estimate her weight more accurately, a best fitting power curve regression for the *Wt* = *f*(*Ht*) relation in 81 female Efé Pygmies was determined (*r* = 0.71). (Data were collected by the Harvard Ituri Project and were made available by R. C. Bailey, N. R. Peacock and members of the project.):

$$Wt = 0.00011 \times Ht^{2.592}$$

In this and other equations, linear measures are in centimetres and weight is in kilogrammes. Height was determined for this female using the tibia and femur⁸ that are published in the description of her skeleton⁹ and her weight was calculated to be 41.4 kg. The corresponding deviation of her femur length from the ape allometric curve, 14%, is considerably less than Jungers thought.

Interestingly, the Mbuti Pygmy femoral deviation is only one-third the deviation for European females¹, raising the possibility that this deviation decreases with decreasing body size. As AL 288-1 is smaller than any living Pygmy by virtually every measure of the trunk or lower limb, the expected femoral deviation from ape allometry for humans this small is of some interest, if only to determine whether the femur of AL 288-1 is smaller than expected for a human of Lucy's diminutive weight. For this purpose, heights were ascertained from femoral and tibial measurements⁸ for 15 published Pygmy skeletons^{9–14} (6 females, 9 males). Weights were calculated for these specimens using the female power curve relation given above, and from a similar power curve calculated for 93 Efé males (the Harvard Ituri Project data) (*r* = 0.67):

$$Wt = 0.00062 \times Ht^{2.241}$$

Using these weights, femoral and humeral deviations from the African ape allometric curve were calculated for the sample. Each set of deviations was used in a regression of deviation as a function of weight. For the humeral deviations the correlation (*r* = 0.56) and regression coefficient were not significant. However, the femoral deviations gave a significant correlation (*r* = 0.83) and regression coefficient

$$D = 0.00042 \times Wt^{2.828}$$

Using this formula, and accepting the 27.3 kg estimate published for Lucy² as Jungers does (this weight is also almost exactly what the male Pygmy formula predicts), the expected femoral deviation for a human of Lucy's weight is 4.9%. The actual AL 288-1 femoral deviation calculated by Jungers is between -2.1% and 0.1%. Thus, Lucy's femur is within about 5% the deviation one would expect in a human of the same size. Instead of using the Pygmy sample alone, an alternative calculation of the expected deviation was attempted using the mean male and female European figures from Jungers¹ and the male and female Pygmy means from the data discussed here. The best fitting power curve for these four points gives an expected femoral deviation of 6.5% for a human of Lucy's size, confirming the above.

Because weight is an estimated quantity for all of the critical data of this (and Jungers') analysis (the Pygmies and the australopithecine in question), a means of ascertaining relative limb length independent of body weight, and independent of the limbs themselves, would be useful. Limb length is traditionally expressed as a percentage of trunk length¹⁵, and some of the vertebrae are preserved for both Lucy and a second female specimen from Sterkfontein, STS 14. The vertebrae comprise the trunk; their heights (and more so the summed heights of each vertebral segment) are significantly correlated with trunk length and body height¹⁶. For instance, the correlation of the full lumbar segment height with skeletal height for six Pygmies with published skeletal heights (that are not estimated from the formula applied to limb lengths)^{11,14} is 0.77 ($P = 0.01$), and the correlation of L3 height (the only lumbar measurable for AL 288-1⁵) with skeletal height is 0.68 ($P = 0.03$). For comparison, the corresponding femur length correlation for this sample is 0.76 ($P = 0.02$). It therefore seems appropriate to use these vertebral dimensions as estimates of trunk length in establishing an independent measure of relative limb length.

Table 1 reports the lengths of the humerus and femur directly, as a percentage of the ventral height of the L3, and as a percentage of the summed ventral heights of the five caudal-most lumbar. The two australopithecines with these data are compared with European Neanderthals (partly because they are said to be short-limbed), all of the published Pygmies with these data¹¹⁻¹⁴, and a sample of Michigan Amerinds. Relative

humerus length for Lucy is close to the Pygmy mean. For both Lucy and the Sterkfontein female, relative femur length is below both the modern means and the Neanderthal mean. However, the difference is not great; relative to the L3, both australopithecines are only 1.3 standard deviations below the Pygmy mean and 1.5 standard deviations below the Michigan Amerind mean, while relative to the total lumbar segment STS 14 (and by inference Lucy) is 1.4 standard deviations below the modern means. Perhaps more importantly, the australopithecines are within the observed range of the Pygmy sample.

Clearly, the femora of AL 288-1 and STS 14 are very short. However, relative to estimates of trunk length they are within the human range, and it would appear that the femora are close to the length expected for humans as small as these diminutive australopithecine females. The humerus of AL 288-1 does not appear to be particularly short, its relative length being close to the Pygmy mean.

While both of Lucy's limbs are within the human range, no individual combines Lucy's proportions. Whether one prefers to call her arms long relative to her legs or her legs short relative to her arms (a better description considering the limb lengths relative to the trunk), the fact is that Lucy had a good deal of mass in her forelimb, and because of the consequent muscularity probably also in the upper trunk. In considering the mechanism of lateral balance during stride, the moment of this mass about the acetabulum was large. This probably explains the very efficient development of the lateral balance mechanism in australopithecines⁴—an example of skeletal/muscular differences that reflect the same pattern of gait. The morphology of the pelvis and femur clearly indicate that this pattern was exclusively bipedalism, irrespective of relative limb length¹⁷. I further suggest, however, that the allometric consequences of this human gait pattern provide a prediction of relatively short hindlimbs in very small hominids with an effective use of stride during bipedal locomotion. For this reason, and because both australopithecines have relative femoral lengths within the modern human range, Lucy's limb proportions cannot be construed as evidence against a fully modern pattern of bipedalism. While I agree with Jungers that "dramatic hindlimb elongation . . . emerges as one of the major evolutionary changes from *A. afarensis* to modern humans", this appears to have been an

Table 1 Limb length in proportion to vertebral body heights

	Ventral body height		Humerus length	H/V	H/SV	Femur length	F/V	F/SV
	L3	Sum for inferior 5 lumbars						
Australopithecines								
AL 288-1	19.3		236.8	12.3	(2.43)*	280	14.5	
STS 14	19.7	97.4				285	14.5	2.93
Neanderthals								
La Chapelle	27.6		313	11.3		430	15.6	
La Ferrassie 1	28.8		340	11.8		458†	15.9	
Shanidar 1	25.0					462†	18.5	
Shanidar 3	26.6	134.7	314	11.8	2.33			
Pygmies								
$\bar{x}$	22.1	110.3	267.1	12.1	2.43	364.2	16.6	3.31
σ	1.6	6.8	16.0	1.1	0.18	22.9	1.6	0.27
Minimum	20.0	98.0	238	10.3	2.09	326	14.2	2.86
Maximum	25.0	121.0	283	14.0	2.75	391.5	19.4	3.79
Michigan Indians (<i>n</i> = 14)								
$\bar{x}$	27.2	136.2	324	11.0	2.35	446	16.4	3.26
σ	1.4	5.9	18.8	0.9	0.16	21.9	1.3	0.23
Minimum	24.0	123.9	285	10.6	2.14	400	14.9	3.01
Maximum	29.6	147.8	352	13.9	2.69	481	19.8	3.83

The ratios are humerus length compared with the ventral height of the lumbar body (H/V), and compared with the summed ventral heights of the inferior five lumbar bodies (H/SV), and the same two ratios for maximum femur length. All measurements are in millimetres.

* Uses STS 14 vertebral sum as an estimate for AL 288-1.

† Determined by E. Trinkaus.

allometric consequence of increasing body size expressed in a hominid with a pattern of gait widely divergent from that of the African apes.

On the other hand, because of the unique proportions of Lucy's limbs relative to each other, the biomechanical requirements of this gait pattern differed somewhat from those for living people. It is possible that Lucy's limb proportions correspond to a different, perhaps broader, locomotor repertoire than is the case today. If, as claimed above, this difference does not lie in the bipedal gait pattern evidenced by the pelvic and hindlimb adaptations, contra Jungers it might be productive to focus on the unique aspects of the australopithecine forelimb.

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Rapid motion aftereffect seen within uniform flickering test fields

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Prolonged viewing of a moving pattern selectively elevates the threshold for a pattern moving in the same direction¹ and induces the classical motion aftereffect (MAE). The aftereffect is seen as a slow drift² in the opposite direction, which is visible even with the eyes shut^{2,3} or while viewing a uniform field^{3,4}. However, as we report here, a strikingly different aftereffect is seen when the test field is uniform and sinusoidally flickered: the field is filled with rapid motion in the direction opposite the adapting motion. This flicker MAE has distinct properties: the adapting grating must be of low spatial frequency; the effect is promoted by high contrast and high temporal frequencies of both adapting and test stimuli; and the aftereffect does not transfer interocularly. In all these respects the flicker MAE differs from the traditional MAE. Motion detectors have been identified in human vision by the threshold detectability^{5,6} and discriminability⁶ of moving patterns and by selective adaptation. The flicker MAE selectively taps a class of transient motion mechanisms that are selective for rapid motion and low spatial frequency. Uniform flicker is an effective stimulus for these mechanisms. It thus appears that the human visual system contains at least two distinct classes of mechanisms for sensing motion.

Stimuli were displayed on a cathode ray tube (CRT) that had a 6 deg diameter field of constant mean luminance (45 cd m^{-2}) with dark surround. The observer stared at a central fixation point and saw a vertical sinusoidal grating that moved rightwards at a rate expressed in Hz. Periodically the adapting grating was replaced by spatially uniform sinusoidal flicker, whose rate (in Hz) was typically the same as that of the adapting grating. The observer pressed a button the instant that the rapid leftward motion aftereffect disappeared from the flickering field. This duration provided a measure of aftereffect strength. Most measurements were done with four to six observers; the results shown here for one or two observers are typical.

For a better impression of the aftereffect, consider the following. The observer adapted to a high-contrast, vertical grating of 0.4 cycle per deg moving rightwards at 8 Hz. The grating filled a 25 deg diameter field, of constant mean luminance. When the adapting grating was turned off, spatially uniform test flicker was presented in only the central 5° of the field. The observer reported that the rapid motion aftereffect was seen only in this central area. However, the aftereffect was seen over the entire field when the flickering region was increased to 25 deg diameter. Thus, the rapid motion aftereffect is seen only on flickering regions, and a very large flickering field may elicit the aftereffect.

Measurements with the 6 deg field demonstrate that the aftereffect is produced only with low spatial frequencies. Figure 1a shows that the aftereffect decreases as the spatial frequency of the adapting grating increases to 3.0 cycles per deg. When the adapting pattern was raised to the next step (4.2 cycles per deg), observer M.C. saw no aftereffect and M.G. saw a fleeting effect that was too brief to measure. The adapting and test rates were 8 Hz, and each adapting grating was 1.3 log units above threshold. Varying the adapting spatial frequency did not seem to change the appearance of the aftereffect, but only affected its duration. The aftereffect is thus obtained only by adapting to patterns below about 4 cycles per deg. This conclusion is reinforced by magnitude estimates⁷ of the initial vividness of the aftereffect. The 0.38 cycles per deg adapting pattern produced the most vivid aftereffect, and vividness decreased as the adapting pattern was raised to 3 cycles per deg.

We next measured the effect of temporal frequency with the adapting pattern at 0.38 cycles per deg. Figure 1b shows that the aftereffect is greatest at the highest rates used, 8 and 16 Hz. The adapting and test rates were the same. Very weak effects were obtained when the adapting pattern was 8 Hz and the test

Fig. 1 Duration (± 1 s.d.) of flicker MAE—the rapid motion seen on a uniform flickering field after adapting to a rightward-moving grating. In a, the spatial frequency of the adapting grating was varied. The rate of motion of the adapting grating and the flicker rate of the test field was 8 Hz. Adapting and test stimuli were set 1.3 log units above threshold. Observers M.C. and M.G. adapted to the moving grating for periods of 15 and 30 s, respectively. In b, the moving adapting grating was held at 0.38 cycle per deg, and the rate of motion of the adapting grating was varied. The adapting and test rates were the same. Stimuli were 1.3 log units above threshold, and the adapting period was 90 s.