but it has been proposed that untranslated RNA molecules are involved. At least two genes which seem to be involved in imprinting, *H19* and *Xist*, produce untranslated RNA products, and a similar transcript is conspicuously located in the locus for Prader–Willi/Angelman syndromes[7]. The imprinting elements must also carry an allele-specific mark which can be put on in the mature germ cells, but which can also be erased during early gametogenesis in the next generation. Although the nature of this signal is not known, mapping studies have identified small regions in the *Igf2* receptor (ref. 3) and *Xist* (refs 8, 9) domains which carry allele-specific methyl moieties that are derived directly from the gametes and are maintained during preimplantation development, and it is not surprising that a similar locus has also been identified near the *H19* gene[10]. □

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LOCOMOTION

Freeloading women

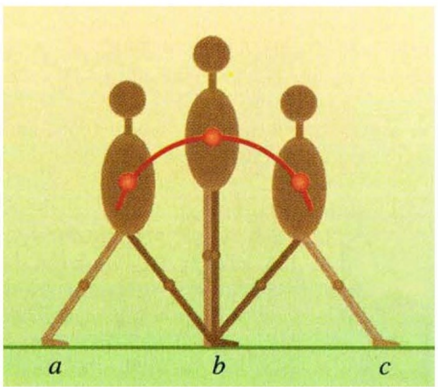
C. Richard Taylor

ALMOST ten years ago, a group including N. C. Heglund and myself found that African women of certain tribes can move heavy loads for free — that is, they can carry up to 20% of their body weight on their heads or supported by a strap looped around their foreheads without expending a single additional calorie[1]. Anyone else pays a high price for carrying such loads, and tires much sooner. Cost increases in direct proportion to the load for both walking and running in most humans[2], and a 20% extra load usually increases energy expenditure by 20%.

So what is the women's trick? The energy-conservation mechanism involved has now been analysed by Heglund and other collaborators (page 52 of this issue[3]). The trick, or at least part of it, is the more efficient use of the body as a pendulum during locomotion.

Energy is conserved during walking, in humans and animals alike, using an inverted pendulum system[4] (see figure). The body speeds and slows, rises and falls, during each step. It reaches its highest speed (and greatest kinetic energy) at its lowest point, when both feet are on the ground (*a* in the figure). Then it pole vaults over one leg, slowing as it rises and converting kinetic energy into gravitational potential energy (*b*). The stored potential energy is converted back into kinetic energy as the body falls and regains its forward speed (*c*). In a perfect pendulum, the energy transfer would be complete (100%) and no muscular work would be needed to maintain a constant speed. In most humans and animals the exchange is pretty good (about 65%), but it is not complete and so the muscles must do a little work in each step to supply the lost energy.

Heglund *et al.*[3] find that the African women increase the efficiency of transfer as they carry heavier loads, whereas European men and women do not. A force platform mounted in a walkway recorded the gravitational potential energy and the forward kinetic energy precisely at each moment, and provided an exact measure of the efficiency of the pendulum. Unfortunately, these experiments do not tell us how efficiency was improved. In any case, relatively more energy is conserved, and relatively less needs to be provided by the muscles.



When walking, everyone uses the pendulum principle to conserve energy. It works by exchanging the body's gravitational and kinetic energy at each step, as discussed in the text, freeing the muscles from some of this work. But the pendulum is usually far from 100% efficient, and muscles consume energy as they replace the mechanical energy lost in the pendulum and as they support the body's weight plus any load. In their paper elsewhere in this issue, Heglund *et al.*[3] describe the finding that certain African women lose progressively less energy as they carry heavier loads, until the pendulum exchange is nearly perfect when the load is about 20% of their weight — hence helping to explain why they can carry these loads for free.

So part of the mystery is solved — but not quite all of it. The problem is that even if the pendulums reached an efficiency of 100%, muscles would have to be active and generate enough force to support the body's weight (plus any load) regardless of whether they shorten and do work or not. The energy cost of generating this force is what determines the cost of running. It can be predicted remarkably well over the entire range of running speeds in animals ranging in size from mice to horses[5] simply from the weight that has to be supported and the time available to support it. The cost of generating force also predicts the cost of walking, even in elephants[6].

There are two ways in which the cost of generating force could be reduced in the African women[7]. The first follows directly from the new finding that they carry out less muscular work. The cost of generating force is lowest when the muscle is isometric and does no work. It increases as the muscle begins to shorten, and is 3–4 times as high at the speed where the shortening muscle works most efficiently. So the cost of generating force decreases as the pendulum becomes more efficient and the work rate of muscles decreases. This leads to a slower shortening velocity and more economical force. The second possibility is a progressively more upright posture with increasing loads, leading to a progressively better mechanical advantage of the limbs against the ground and to less muscle being required to support the body's weight (plus load).

The remaining question is how force is generated more cheaply. This could be answered by combining high-speed film and video analysis with the force platform analysis. Once we have the answer, it should be possible for all of us to emulate these remarkable women and carry heavy loads for free. □

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