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- Mackenzie, F. T. & Garrels, R. M. *Am. J. Sci.* **264**, 507–525 (1966).
- Smith, S. V. & Hollibaugh, G. T. *Rev. Geophys.* **31**, 75–89 (1993).

- Williams, P. M. & Druffel, E. R. M. *Nature* **330**, 246–248 (1987).
- Raymond, P. A. & Bauer, J. E. *Nature* **409**, 497–500 (2001).
- Hedges, J. I., Keil, R. G. & Benner, R. *Org. Geochem.* **27**, 195–212 (1997).
- Ludwig, W., Probst, J.-L. & Kempe, S. *Glob. Biogeochem. Cycles* **10**, 23–41 (1996).
- Kao, S. & Liu, K. *Limnol. Oceanogr.* **41**, 1749–1757 (1996).
- McClain, M. E., Richey, J. E. & Brandes, J. A. *Glob. Biogeochem. Cycles* **11**, 295–311 (1997).

Biomechanics

Walking on other planets

Alberto E. Minetti

A nineteenth-century equation used for building model ships allows us to compare the motion of animals of different sizes and gaits. It may also give us an idea of how we would move on different planets.

What do a gibbon swinging by its arms from tree to tree, a sailing steamship, and a walking human have in common? The answer lies in a simple concept introduced in the nineteenth century by nautical engineer William Froude to help him to produce model ships that maintained the same propulsion dynamics as full-size vessels. His 'Froude number' is a dimensionless variable that was brought into biology by D'Arcy Thompson¹ and popularized by McNeill Alexander^{2,3} in the study of the energetics and mechanics of animal locomotion. This number allows one to compare the motion of species with different numbers of legs and gaits, and to investigate the effects of different body sizes on the mechanics of movement. As suggested by various earlier papers^{4–6}, and borne out by new work described by Cavagna and colleagues in the *Journal of Physiology*⁷, the Froude number is also a reliable rule-of-thumb for predicting walking speeds on planets with gravities different from that of the Earth.

In walking humans or swinging gibbons, changes in the vertical position of the body's centre of mass during movement affect the gravitational potential energy of the body, and are accompanied by opposite changes in the kinetic energy needed to drive movement. The result is a pendulum-like mode of movement that saves mechanical energy. Roughly the same principles apply to ships, but here the potential energy is related to the size of the wave generated by the ship.

One of the theories underlying studies of movement — dynamic similarity³ — basically states that geometrically similar bodies that rely on pendulum-like mechanics of movement will have similar gait dynamics if the Froude number remains the same. This number (Fr) is given by $Fr = v^2 / (g \times l)$, where v is the speed of movement (in $m\ s^{-1}$), g is acceleration due to gravity (in $m\ s^{-2}$) and l is a characteristic length (such as leg length, in metres). The Froude number is directly proportional to

the ratio between the kinetic energy and the gravitational potential energy needed during movement.

Dynamic similarity implies that, for example, despite differences in body size and

number of legs, humans and quadrupeds change from walk to run or trot at the same Froude number, close to 0.5 (ref. 3). Even gibbons⁸ change from merely swinging to swinging with aerial phases at Froude numbers ranging from 0.3 to 0.6. Humans of short height, such as children^{9,10}, patients suffering from early-onset growth-hormone deficiency¹¹ and pygmies¹², optimally walk at speeds that correspond dynamically to that for adults, that is, with a Froude number of 0.25. Here, walking speed is optimal when the recovery of energy by the body — by exchanging potential and kinetic energies — is maximal⁷. What all of this means is that, within the same gravitational environment (such as on the Earth), the smaller the body, the lower the 'equivalent' speed of movement, which is proportional to the square root of the leg length.

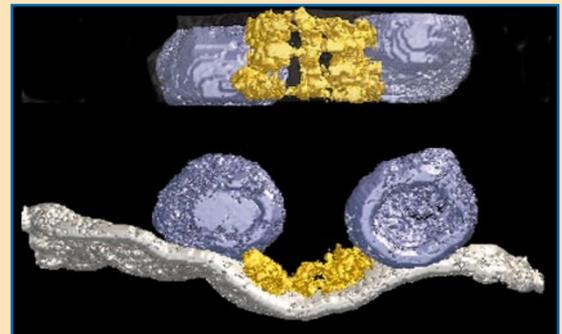
But the power of the Froude number for predicting equivalent walking speeds is not confined to the Earth. Within the same species and for a given body size, dynamic

Neurobiology

Activity at the active zone

Presynaptic active zones are the specialized sites from which nerves release neurotransmitter. They are characterized by the presence of calcium channels, synaptic vesicles containing neurotransmitter, and aggregates of protein that make up what is known as 'active-zone material'. This material was described by S. L. Palay almost 50 years ago (*J. Biophys. Biochem. Cytol.* **2**, 193–202; 1956), but its precise structure and function have remained an enigma. Things may be about to change, however, thanks to the publication elsewhere in this issue of stunning three-dimensional reconstructions of the frog neuromuscular junction (*Nature* **409**, 479–484; 2001).

To study this junction between nerve and muscle, M. L. Harlow and colleagues used a technique known as electron microscope tomography, which gives greater spatial resolution than conventional transmission electron microscopy. They describe three distinct elongate structures — which they call ribs, beams and pegs — that make up the first 15 nanometres



of active-zone material as one looks into the neuron. The top image shows this view, with the active-zone material in yellow and the synaptic vesicles in blue.

Beams — which make up the vertical band in the centre of this image — are arranged along the long axis of the elongate active zone, and form the backbone of the structure. Ribs lie perpendicular to this long axis, and link the central backbone to the double row of synaptic vesicles that straddle it. Pegs (not apparent in these images) tether each rib to the plasma membrane in a pattern that matches the distribution of molecules that are thought to be calcium channels. The lower image is a side-on view, with the presynaptic plasma

membrane in grey. The structure is perhaps best appreciated in the movies published on *Nature's* web site (<http://www.nature.com/nature/>).

As a whole, the active-zone material appears to provide a scaffold by which synaptic vesicles are localized to the specialized presynaptic membrane. But the proteins that make up the structure probably have more specific functions. The intracellular domains of calcium channels may form all or part of the pegs, and ribs may be composed of the host of proteins that together mediate docking and fusion of vesicles with the presynaptic membrane. We eagerly await the formal identification of the rib, beam and peg proteins. **Lesley Anson**

M. L. HARLOW ET AL.

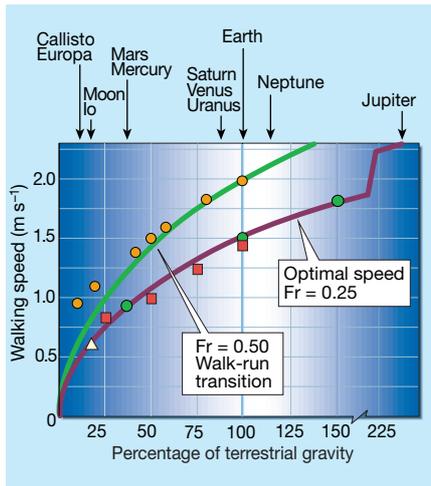


Figure 1 Walking speed as a function of gravity. The curves represent the predictions of the theory of dynamic similarity. These predictions were made using the Froude-number equation, $Fr = v^2/(g \times l)$, where v is the velocity in $m\ s^{-1}$, g is the acceleration due to gravity in $m\ s^{-2}$, l is 0.92 m (the average leg length for adult male humans), and Fr is 0.25 (which sets the optimal walking speed on Earth^{9–12}) or 0.5 (at which humans move spontaneously from a walk to a run on Earth³). Squares and orange circles refer to measurements of optimal walking speeds⁴ and walk-to-run-transition speeds⁵, respectively, in simulated low-gravity conditions. The triangle represents a previous estimate of reduced walking speed on the Moon¹³. Green circles represent recent measurements of optimal speed obtained using parabolic flight to simulate low- and high-gravity conditions^{6,7}.

similarity also predicts that the lower the gravity, the slower the equivalent walking speed, which depends on the square root of the gravity ratio — the gravity of the planet in question divided by that of the Earth. On Earth, the optimal walking speed and walk-to-run-transition speed for an adult man of average height are, respectively, about 1.5 and 2.0 $m\ s^{-1}$. Figure 1 shows the relationships between walking speed and gravity at Froude numbers of 0.25 (which determines the optimal walking speed for humans) and 0.5 (which determines the walk-to-run-transition speed). One can use the Froude number to predict that the corresponding speeds on a stellar body with 16% of the Earth's gravity, such as the Moon, will be about 40% (the square root of 16%) of those on Earth — that is, about 0.6 and 0.8 $m\ s^{-1}$, respectively.

These values were also predicted on the basis of a different approach about 35 years ago¹³, and the impossibility of walking at terrestrial speeds on the Moon has been clear to see in debriefings from the Apollo missions¹⁴. Moreover, experimental evidence has confirmed the predictive power of the Froude number in low gravity. Different low-gravity conditions have been simulated

in the lab by applying a nearly constant upward force to the waist of subjects walking on a motorized treadmill^{4,5}. As predicted, the optimal walking speed⁴ and the spontaneous transition between walking and running⁵ occurred at Froude numbers close to 0.25 and 0.5, respectively. The slight discrepancy observed at low gravity (Fig. 1) is likely to be caused by the approximate nature of the simulation — limbs were allowed to swing normally, as if still affected by terrestrial gravity.

Cavagna *et al.*⁷ now go further, to look at the mechanics of human walking in both low and high gravity. The low-gravity conditions correspond to those on Mars, being 40% of the Earth value. The high-gravity value was 150% of that on Earth. The authors used given portions of the parabolic trajectory of an aeroplane equipped with platforms that were sensitive to forces in all directions. In this way, Cavagna *et al.* measured the displacement of the body's centre of mass during a couple of walking steps at different constant gravities and walking speeds. From these measurements, they calculated the recovery of energy. They also recorded the speeds at which energy recovery was optimal (the optimal walking speeds). These speeds closely match those predicted when the Froude number is 0.25 (ref. 15), although the range of optimal speeds in high gravity is quite broad.

Indeed, Cavagna *et al.* conclude that increased gravity increases the range of walking speeds. This is again predicted by the Froude number, as seen in Fig. 1, where the vertical distance between the curves increases with increasing gravity. Here, the vertical distance represents the range of speeds within two dynamically different conditions.

Plant biology

Floral quartets

Günter Theißen and Heinz Saedler

Goethe was right when he proposed that flowers are modified leaves. It seems that four genes involved in plant development must be expressed together to turn leaves into floral organs.

What controls the difference between a plant's floral organs and its leaves? Over 200 years ago Johann Wolfgang von Goethe proposed that the different parts of a plant result from 'metamorphosis' (meaning transformation) of a basic organ, the 'ideal leaf'. But if floral organs are just modified leaves, what are the modifiers? On page 525 of this issue¹ Honma and Goto provide the answer in molecular terms.

A typical flower consists of four different types of organ arranged in four whorls (Fig. 1, overleaf). There are leaf-like sepals in the outermost whorl; showy petals in the second

Bipedal and quadrupedal walking — unlike swinging — remain an approximation of ideal pendulum dynamics. Despite this, the Froude number, and the underlying theory of dynamic similarity, has so far proved a handy rule-of-thumb for predicting equivalent walking speeds as a function of body size or gravity. It is not yet known to what extent faster walking speeds can be maintained in high gravity for more than the few steps studied by Cavagna *et al.*⁷. But it is nonetheless impressive that an idea introduced in the nineteenth century to produce model ships can be used in the twenty-first century to predict how humans would walk on other planets.

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- Thompson, D. W. *On Growth and Form* (Cambridge Univ. Press, 1961).
- Alexander, R. M. *Nature* **261**, 129–130 (1976).
- Alexander, R. M. *Physiol. Rev.* **69**, 1199–1227 (1989).
- Griffin, T. M., Tolani, N. A. & Kram, R. *J. Appl. Physiol.* **86**, 383–390 (1999).
- Kram, R., Domingo, A. & Ferris, D. J. *Exp. Biol.* **200**, 821–826 (1997).
- Cavagna, G., Willems, P. A. & Heglund, N. C. *Nature* **393**, 636 (1998).
- Cavagna, G., Willems, P. A. & Heglund, N. C. *J. Physiol. (Lond.)* **528**, 657–668 (2000).
- Cheng, Y. H., Bertram J. E. & Lee, D. V. *Am. J. Phys. Anthropol.* **113**, 201–216 (2000).
- Cavagna, G. P., Franzetti, P. & Fuchimoto, T. *J. Physiol. (Lond.)* **343**, 232–339 (1983).
- Dejaeger, D., Willems, P. A. & Heglund, N. C. *Pflügers Arch. Eur. J. Physiol.* **441**, 538–543 (2001).
- Minetti, A. E., Ardigo, L. P., Saibene, F., Ferrero, S. & Sartorio, A. *Eur. J. Endocr.* **142**, 35–41 (2000).
- Minetti, A. E. *et al. Eur. J. Appl. Physiol.* **68**, 285–290 (1994).
- Margaria, R. & Cavagna, G. *Aerospace Med.* **35**, 1140–1146 (1964).
- Minetti, A. E. *Proc. R. Soc. Lond. B* **265**, 1227–1235 (1998).
- Minetti, A. E. *Acta Astron.* (in the press).