Horsepower from a horse

SIR — Recent studies of flying animals carrying loads[1] and of skeletal muscle *in vitro* subject to cyclic motion[2] suggest that the maximum sustainable mechanical power per kg of muscle is 100 – 200 W. Given an animal's size and its proportion of muscle mass, it is thus possible to calculate an upper limit to an animal's power output. This led us to wonder how much horsepower one horse can actually produce.

The body mass of horses varies from less than 100 kg for ponies to more than 800 kg for large draught animals. According to Munro[3], skeletal muscle for a horse is about 45 per cent of the total mass, but we estimate that only 30 per cent could be used for mechanical work at any one moment. Assuming a mass-specific rate of 100 W kg^{-1} of muscle and a body mass of 600 kg, one horse could, in theory, produce 18,000 W or, since one horsepower (HP) equals 746 W, about 24 HP! Is is possible that one horse generates that much horsepower? The assumptions, in the worst case, might inflate the result by a factor of 2, yet this still gives an estimate of about 12 HP. This raises the question: was the definition of horsepower based on a lower rate of work, or can a healthy horse actually produce more than 10 HP?

As to the first possibility, it was James Watt himself who defined horsepower. According to Dickinson[4], in the early 1780s Boulton and Watt were manufacturing rotary steam engines that replaced horse gins. Quite naturally, payment for the engine was an annual premium based on the number of horses needed to do the equivalent amount of work. In discussions with millwrights, Watt learned that during a day's work a horse would walk an average of two and a half times per minute around a 24-ft diameter mill wheel. Dickinson[4] (p. 145) says Watt assumed a horse exerted a tractive effort of 180 pound force (lbf), yielding a power estimate of 33,929 ft-lbf min^{-1} (power = force × distance/time). In Watt's blotting and calculation book this number was rounded to 33,000 ft-lbf min^{-1}, equivalent to the more familiar definition for HP of 550 ft-lbf s^{-1}. (The US Bureau of Standards[5] gives a different account of Watt's calculation that says he considered engine friction.) By either calculation, Watt's measure of power output is clearly based on a rate that horses could maintain for a full day, not a peak performance.

As to the second possibility, Collins and Caine[6] list data from the horse pulling contest at the 1925 Iowa State Fair showing that peak mechanical power output of a horse is 12–14.9 HP. This effort lasted only a matter of seconds and is probably a realistic estimate of peak performance. Similar maximal rates, when expressed per kg of body mass, have been documented in human athletes[7].

Why is the daily work rate so much lower? Collins and Caine[6] suggest that a draught horse should pull 10 per cent of its body weight at a rate of 2.5–3 miles h^{-1} (10-hour working day) to maintain health and vigour. Comparable working rates were suggested by Youatt[8] in 1826. Interestingly enough, both these work rates are just about 1 HP. Furthermore, they correspond to a daily metabolic rate of about 4 times the basal rate, which is a rate that has been documented in other vertebrates performing sustained activity[9,10]. In summary, it seems that the millwrights of the 1780s knew how to keep their animals in good shape, that Watt made his estimates carefully, and that a horse can provide significantly more than one horsepower.

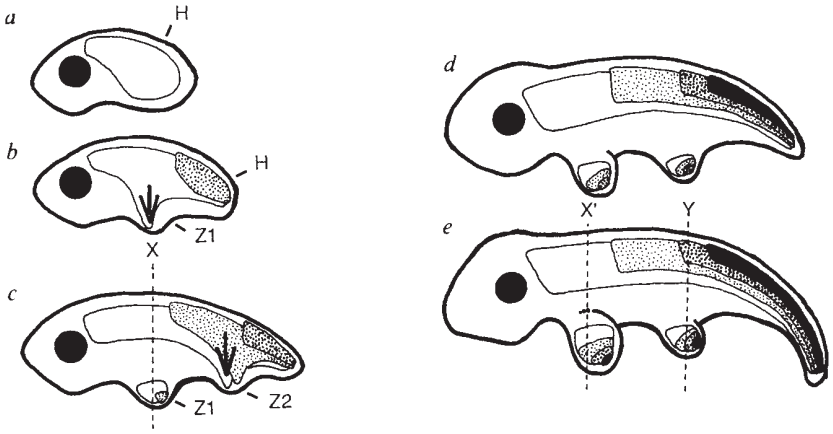
R. D. Stevenson
Department of Biology,
University of Massachusetts at Boston,
Boston,
Massachusetts 02125-3393, USA
Richard J. Wassersug
Department of Anatomy & Neurobiology,
Dalhousie University, Halifax,
Nova Scotia B3H 4H7, Canada

1. Ellington, C. P. *J. exp. Biol.* **160**, 71–91 (1991).
2. Stevenson, R. D. & Josephson, R. K. *J. exp. Biol.* **149**, 61–78 (1990).
3. Munro, H. N. (ed.) in *Mammalian Protein Metabolism* 133–182 (Academic, New York, 1969).
4. Dickinson, H. W. *James Watt* (David & Charles, Newton Abbot, 1967).
5. US Dept. of Commerce *Cir. Bureau Stand.* **34** (1912).
6. Collins, E. V. & Caine, A. B. *Iowa Agri. exp. Sta. Bull.* **240**, 193–223 (1926).
7. Vandewalle, H., Peres, G., Heller, J., Panel, J. & Monod, H. *Eur. J. appl. Physiol.* **56**, 650–656 (1987).
8. Youatt, W. *The Horse* (Knight & Co, London, 1846).
9. Drent, R. H. & Daan, S. *Ardea* **68**, 225–252 (1980).
10. Peterson, C. C., Nagy, K. A. & Diamond, J. *Proc. natn. Acad. Sci. U.S.A.* **87**, 2324–2328 (1990).

Hox genes, fin folds and symmetry

SIR — Tabin and Laufer[1] suggest an evolutionary explanation of the similarity between tetrapod fore and hind limbs in which the *Hox* gene-regulated limb pattern originated in the pelvic appendage, and subsequent ectopic activation imposed the regulation and resultant homeotic transformation on the ancestral pectoral fin/fore limb. I agree with the general proposal that patterns of genetic regulation provide a new level of explanation for homology[2], but I question Tabin and Laufer's specific evolutionary hypothesis.

The 'pelvic before pectoral limb' evolutionary model is based partly on the continuous lateral fin-fold theory of the origin of paired vertebrate appendages,



Schematic representation of spatial and temporal (*a*–*e*) sequential overlapping *Hox* gene expression domains in a developing vertebrate embryo (from refs 2, 8 in ref. 1). Black dot, cranial region; arrows, mesoderm migrating laterally into emergent limb bud; thin outlines delimit *Hox* gene expression domains in limb buds and trunk/caudal regions (shaded from clear, stippled to black). Maintenance and elaboration of *Hox* gene expression along cranio-caudal and limb-outgrowth axes appears to be influenced by a unified system[14] in which signalling activity emerges from centre H, and spreads into flank tissue centres Z1 and Z2 (ref. 14), with peak activity occurring in pectoral before pelvic limb fields. At an early stage (*c*), *Hox* gene expression in the pectoral limb bud mesoderm resembles that in the axial mesoderm (section X) because the former is derived from the latter. At a later state (*e*) increased dissimilarity between the expression patterns (section X') results from the fixed anterior position and continued distal development of the pectoral limb bud, and the elaboration of trunk *Hox* gene expression in more posterior axial mesoderm. Initiation of the pelvic limb bud at a later stage incorporates posterior axial mesoderm in which a fuller complement of *Hox* genes has either already been or will be expressed. Position in the posterior flank region leads to closer similarity of expression pattern with adjacent mesoderm (section Y). As the activity of Z1 peaks before Z2 during ontogeny, a similar sequence is argued to have occurred in phylogeny. Contrary to the suggestion in ref. 1, no homeotic transformations, translations of signalling centres between fins, taxa with continuous lateral fin folds or with pelvic but without pectoral fins[3], are required. However, differences remain between the *Hox* expression patterns predicted by this alternative hypothesis and those few which are actually known. Here, anterior-most genes expressed axially have principal expression in the limb buds, followed by the remainder of the *Hox* network, whereas in known amniote limb buds only the posterior members of clusters *A* and *D* of the *Hox* network are expressed.