

unknown craton to the north, and a succeeding rift took place at the southern periphery of that northern craton and its southern offset including the Aksu blueschist terrain adjoined the proto-Tarim craton. The former indicates southward subduction and the latter northward subduction. Whatever the direction of subduction the evolution of the Tarim craton involved a high-pressure low-temperature subduction metamorphism at 700 Myr. □

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## Energetics of running: a new perspective

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THE amount of energy used to run a mile is nearly the same whether it is run at top speed or at a leisurely pace (although it is used more rapidly at the higher speed). This puzzling independence of energy cost and speed is found generally among running animals<sup>1</sup>, although, on a per gram basis, cost is much higher for smaller animals. Running involves little work against the environment<sup>2</sup>; work is done by muscles and tendons to lift and accelerate the body and limbs. Some of the work is recovered from muscle-tendon springs without metabolic cost<sup>3,4</sup> and work rate does not parallel metabolic rate with either speed or size. Regardless of the amount of work muscles do, they must be activated and develop force to support the weight of the body. Load-carrying experiments have shown that the cost of supporting an extra newton of load is the same as the weight-specific cost of running<sup>5</sup>. Size differences in cost are proportional to stride frequency at equivalent speeds, suggesting that the time available for developing force is important in determining cost<sup>6,7</sup>. We report a simple inverse relationship between the rate of energy used for running and the time the foot applies force to the ground during each stride. These results support the hypothesis<sup>8</sup> that it is primarily the cost of supporting the animal's weight and the time course of generating this force that determines the cost of running.

In testing the above hypothesis across both speed and size, we made three assumptions. First, we assumed that most of the

force exerted by the muscles acts to oppose gravity. This seems reasonable as force platform measurements on a variety of running animals have shown that the vertical force is at least 10 times the horizontal force<sup>9</sup>, and the average vertical force during a stride must be equal to the weight of the animal ( $W_b$ ). Next, we assumed that a unit volume of active muscle exerts the same force on the ground regardless of speed or animal size. A recent study<sup>10</sup> supports this assumption for both speed and size. Although the mechanical advantage is worse in smaller animals, they have correspondingly shorter muscle fibres<sup>11</sup>, and force per cross sectional area is constant. Finally, we assumed that muscles operate over similar ranges of the force-velocity relationship, irrespective of speed and size. This requires faster fibres at higher speeds and in smaller animals, because the force is applied in a shorter period of time. It costs more for faster fibres to generate force because their cross-bridges cycle and consume ATP at faster rates<sup>12,13</sup>.

The hypothesis states that the rate of energy consumption per newton of body weight by the muscles of a running animal ( $\dot{E}_{metab}/W_b$ ) is inversely proportional to the weight-specific rate of force application,  $W_b/t_c$  divided by  $W_b$ , where  $t_c$  is the time for which the foot applies force to the ground during each stride. So

$$\dot{E}_{metab}/W_b = c \cdot 1/t_c \quad (1)$$

where  $c$  is a cost coefficient. This hypothesis can be tested by measuring  $\dot{E}_{metab}$  and  $t_c$  over a range of speeds and gaits in animals of different sizes.

Our hypothesis should also account for the size-related difference in the cost of transport, the amount of energy consumed to move a unit weight a unit distance. The cost of transport,  $E_{trans}/W_b$ , is simply weight-specific rate of energy

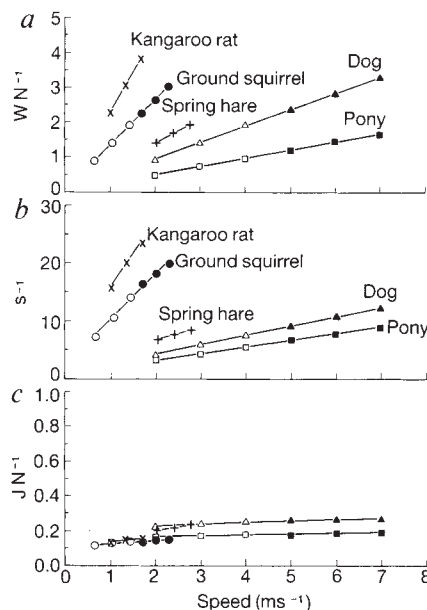


FIG. 1 Weight-specific rates of energy consumption ( $\dot{E}_{metab}/W_b$ , panel a) and force application ( $1/t_c$ , panel b) increase linearly over the entire range of running speeds in a diverse assortment of mammals, ranging in size from 30-g kangaroo rats to 140-kg ponies. The ratio of these two is a cost coefficient (panel c) that can be used to calculate the rate of energy consumption of a running animal knowing only body weight ( $W_b$ ) and the time per stride that a single foot is in contact with the ground ( $t_c$ ). The cost coefficient is nearly constant across speed and size, indicating that metabolic rate is inversely proportional to the time of force application. Open symbols, trotting; closed symbols, galloping; crossed symbols, bipedal hopping. The three points for each gait show the average for all the individuals (see text) at slow, medium and fast speeds within each gait. Lines are linear least-squares regressions.

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consumption divided by running speed,  $v$ :

$$E_{\text{trans}}/W_b = \frac{\dot{E}_{\text{metab}}}{W_b \cdot v} \quad (2)$$

Running speed is equal to step length, the distance travelled while each foot is in contact with the ground ( $L_c$ ), divided by  $t_c$ :

$$v = L_c/t_c \quad (3)$$

We can combine equations (1), (2) and (3) to solve for  $E_{\text{trans}}/W_b$  in terms of  $L_c$ :

$$E_{\text{trans}}/W_b = c \cdot 1/L_c \quad (4)$$

Thus, we predict larger animals with longer legs and step lengths will have lower transport costs.

We used a comparative approach to test this hypothesis, taking advantage of the two- to three-fold change in metabolic rate with speed and a 10-fold difference in cost of transport across animal size. Steady-state oxygen consumption and average time of foot contact were measured over the range of aerobic running speeds in kangaroo rats (*Dipodomys merriami*, 32 g), ground squirrels (*Spermophilus tridecemlineatus*, 210 g), spring hares (*Pedetes capensis*, 3.0 kg), dogs (*Canis familiaris*, 25.8 kg) and ponies (*Equus caballus*, 141 kg). Oxygen consumption was measured while animals ran at a constant speed on a treadmill using an open flow system described by Fedak *et al.*<sup>14</sup>. We subtracted the extrapolated oxygen consumption at zero speed from the measured value, assuming that the additional energy is used by the muscles for running<sup>15</sup>. To calculate rate of energy consumption we assumed 20.1 joules of energy are liberated for each ml of oxygen consumed. The time of contact,  $t_c$ , was measured for each limb from high-speed ciné films (Photosonics 16 mm 1PL, 200 frames  $s^{-1}$ ), or force platforms<sup>9,16</sup> (in the case of the bipeds) and averaged for the total number of limbs. Oxygen consumption and  $t_c$  were measured on the same individuals. Some of the measurements of oxygen consumption have been reported previously<sup>17,18</sup>. Weight-specific rates of energy consumption (Fig. 1a) and force application (Fig. 1b) both increased linearly with speed. Our measurements of oxygen consumption agree well with the general allometric equation<sup>19</sup>. Using equation (1), we calculated the cost coefficient for each animal at each speed, by dividing  $\dot{E}_{\text{metab}}/W_b$  by  $1/t_c$  (Fig. 1c). As predicted by the hypothesis, this coefficient was nearly constant across speed and about the same value for the different species.

We found that  $L_c$  increased only slightly over each animal's aerobic speed range (Fig. 2). This explains the initial paradox—why the same amount of energy is consumed in running a mile

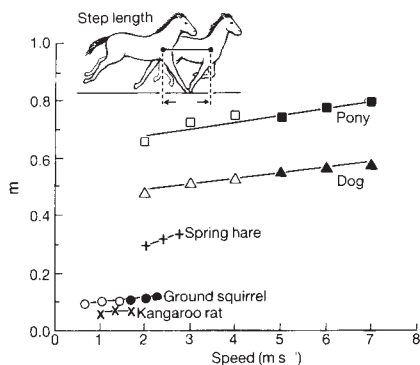


FIG. 2 Step length,  $L_c$  (the distance the body moves forward during the time a single foot is on the ground per stride), increases very little as speed increases but is greater in larger animals. Symbols here are as in Fig. 1. We use the term step length, as defined by Gray<sup>22</sup>, whereas others have used it to mean half of a stride.

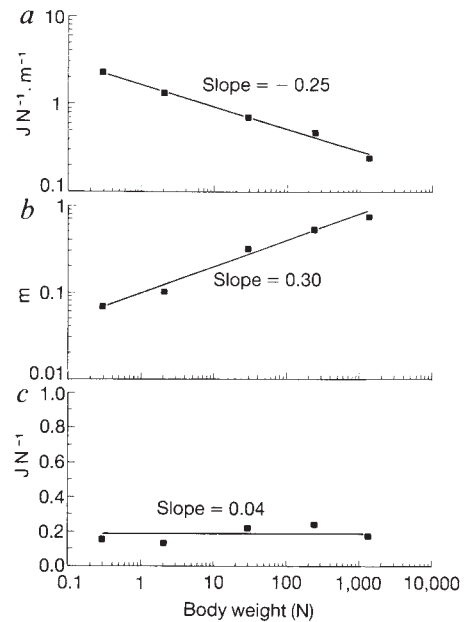


FIG. 3 Cost of transport ( $E_{\text{trans}}/W_b$ , panel a)—the amount of energy consumed in moving a unit of body weight a unit distance—decreases and step length ( $L_c$ , panel b) increases with increasing body weight. The product of cost of transport and step length is a cost coefficient ( $c$ , panel c) that is independent of animal size, indicating that cost of transport is inversely proportional to step length. The step-length value plotted in panel b is either the middle trotting or hopping speed.

regardless of speed. Using equations (2) and (3) we see that  $E_{\text{trans}}/W_b$  will be independent of speed if  $L_c$  is constant. Step length increased in a regular, almost geometrical manner with body weight. When plotted on logarithmic coordinates,  $L_c$  increases linearly with body weight with a slope of 0.30 (95% confidence limits,  $\pm 0.05$ ) (Fig. 3b). This slope agrees with values reported for other species<sup>20</sup>. The cost of transport,  $E_{\text{trans}}/W_b$ , decreased with increasing body weight (Fig. 3a). When plotted on logarithmic coordinates this is a linear relationship with a slope of  $-0.25 (\pm 0.09)$ , a value similar to previous reports<sup>19,21</sup>. The ratio of  $E_{\text{trans}}/W_b$  to  $1/L_c$  equals  $c$ . As predicted by equation (4),  $c$  is nearly constant over the range of body size with no indication of a size dependency (mean of  $0.183 \text{ J N}^{-1}$ , s.d. of 0.045) (Fig. 3c). There is remarkably little variation in this cost coefficient, considering  $E_{\text{trans}}/W_b$  varies by 10-fold.

Apart from shedding light on the energetics of locomotion, our findings may be of practical use to ecologists interested in field estimates of energy consumption. A measurement of  $t_c$  from films and a knowledge of the weight of an animal can provide a good approximation of its rate of energy consumption and cost of transport. Our measurements of the metabolic cost of running and  $t_c$  show that the simple hypothesis formalized in equation (1) works remarkably well in mammals ranging in size from 30 g kangaroo rats to 140 kg horses. We conclude that the cost of running is primarily determined by the cost of supporting weight and by the time course of force application. □

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## Spatial representation of words in the brain implied by studies of a unilateral neglect patient

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READING and writing require access to stored knowledge about the spelling of words. Presumably, we recognize *chair* but not *chare* or *chiar* as a word of English, and similarly would write 'chair' but not 'chare' or 'chiar', because we access orthographic representations that specify the identity and the order of the graphemes (abstract letter representations) that comprise the spelling of words<sup>1,2</sup>. Thus, a fundamental problem concerns the content and structure of the hypothesized orthographic representations, and how information about grapheme order is represented and processed. We present evidence from a brain-damaged patient (N.G.) with unilateral neglect that this information is coded spatially. Unilateral neglect is a disorder clinically characterized by the inability to perceive or respond to stimuli presented to the side contralateral to the site of lesion, despite the absence of significant sensory or motor deficits<sup>3,4</sup>. The patient made reading and spelling errors only on the right half of words, regardless of length. Furthermore, she produced the same pattern of errors in reading and spelling, irrespective of the topographic arrangement of stimuli in reading (horizontal, vertical or mirror-reversed words) and of the type of response in spelling (written, oral or backward oral spelling). This pattern of performance suggests that order information in orthographic representations is coded spatially in a word-centred coordinate system; that is, in a spatially defined coordinate frame whose centre corresponds to the midpoint of a canonical, orientation-invariant representation of the word and not the midpoint of the word stimulus<sup>5</sup>.

N.G. is a 77-year-old left-handed woman, who presented with a particularly pure clinical picture of unilateral neglect due to a stroke involving a large area of the left parietal white matter and the left anterior basal ganglia, adjacent to the head of the caudate nucleus (as revealed by CT scan). In contrast to her normal spoken language, eye movements and visual fields, N.G. showed severe difficulties in processing the right side of objects and words: in bisecting lines she systematically displaced the centre to the left; in drawing objects from memory she omitted or distorted details on the right side; and in reading and writing she made errors only on the right side of words. The right-sided reading errors persisted even when it could be demonstrated that she had processed the whole word, as revealed by her flawless ability to name all the letters in the word. Similarly, her bisection displacement persisted even after she successfully indicated the extremities of the line before bisecting it (see Fig. 1). Thus, N.G.'s unilateral neglect seemed to reflect a deficit in processing the right side of internal representations and not a deficit in sensory processing or stimulus scanning<sup>6-13</sup>.

N.G. was asked to read and write several thousand words of various lengths in various tasks ( $n = 2,202$  and 1,662, respectively). The stimuli used in the various tasks were selected from word lists controlled for standard lexical and non-lexical factors known to affect reading and spelling performance, such as word and stem frequency, grammatical class, length, concreteness, and morphological structure. The lists were compiled from The Johns Hopkins Dyslexia and Morphology Batteries. Overall accuracy was 77% in reading and 24% in spelling. The only factor to affect performance in reading was frequency—N.G. read high-frequency words with greater accuracy than low-frequency words. The only factor to affect spelling was length, as she spelled short words with greater accuracy than long words. Furthermore, errors were only made on the right half of a word, and these increased linearly as a function of absolute distance in graphemes from the centre of the word (Table 1). This result was independent of the form of stimulus input in reading and the form of output in spelling, that is, N.G. produced virtually identical rates and distributions of errors in reading words presented in horizontal, vertical or mirror reversed form. She also produced essentially identical rates and distributions of errors in written, oral and backward-oral spelling of words. The distribution of errors as a function of letter position in a word was virtually identical across all reading and spelling tasks (Table 2). Examples of N.G.'s performance in the various reading and spelling tasks are shown in Fig. 1. In all tasks, her errors were restricted to the 'right' end of canonical representations of words.

Although other brain-damaged subjects have been described whose reading performance is similar to that of N.G.<sup>6,9,10,12,13</sup>, none of these showed a spatially-specific deficit which (where tested) remained invariant—always involved the same end of the word—under topographic transformations of the stimulus

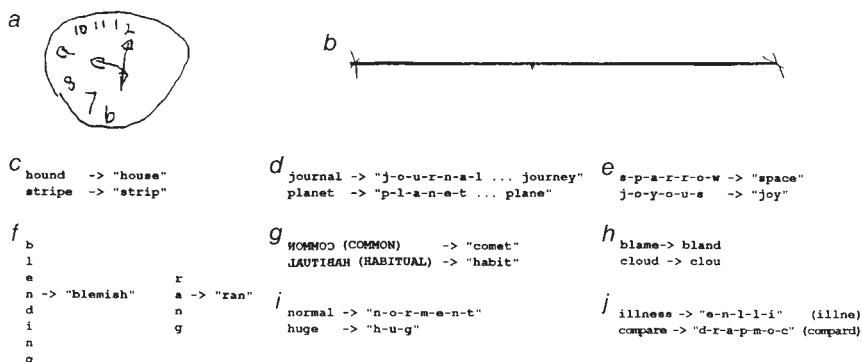


FIG. 1 Examples of N.G.'s performance in various tasks. *a* Attempt to draw a clock; *b* bisection of a 5-inch line after having indicated the extremities. The centre is shifted to the left, indicating neglect of the right end of the line; *c*, reading horizontally displayed words; *d*, reading horizontally displayed words after naming the letters in the words; *e*, naming orally spelled words; *f*, reading vertically displayed words; *g*, reading mirror-reversed words; *h*, written spelling; *i*, oral spelling; *j*, backward oral spelling. Note that in all cases errors only involved the right half of a canonical, word-centred representation of the word, and not the right half of a viewer-centred representation (compare horizontal and vertical, and mirror-reversed conditions in reading) or the last letters produced (compare oral and backward oral spelling).