

have the last word, and our ideas about stability and structure of very neutron-rich nuclei will change in the next few years. □

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Biomechanics

Wallabies vibrate to breathe

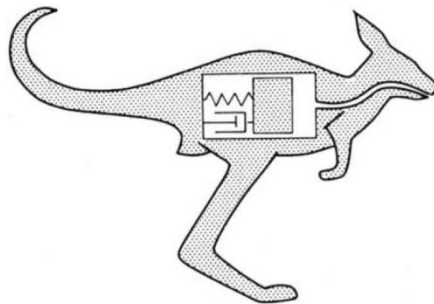
R. McNeill Alexander

WALLABIES take one breath per hop throughout their range of hopping speeds. Baudinette and his colleagues at Flinders University¹ demonstrate this result in experiments in which the wallabies hopped on a motorized treadmill. They suggest that the respiratory system is a mechanical oscillator and breathing is largely passive, driven by hopping movements.

Similar suggestions have been made for horses, dogs and jackrabbits, which take one breath per stride when they gallop². But wallabies are more convenient subjects because they travel on just two legs which move in phase with each other (see photograph), making it easier to interpret the data. Galloping quadrupeds move each leg out of phase with all the rest and have correspondingly complicated patterns of acceleration and deceleration³. People also coordinate breathing movements with their running movements, but usually take two strides per breath.

The hypothetical oscillator of wallabies is shown in the sketch. The movable mass inside the animal represents the abdominal viscera, which move posteriorly as the lungs fill and anteriorly as they empty. It is mounted on a spring, which represents the elastic properties of the diaphragm and other tissues, and a dashpot, which represents the damping effects of tissue and air viscosity. Diagrams like this appear in engineering textbooks, representing accelerometers and seismometers⁴. If the spring were stiff enough to make the natural frequency of the system much higher than the hopping frequency, the viscera would behave like an accelerometer. They would make only

small movements relative to the skeleton, and their displacement at any instant would be proportional to the body's acceleration. The lungs would be fullest at the instant of peak forward acceleration. However, if the spring were compliant enough to make the natural frequency of



the viscera much lower than the hopping frequency, they would act like a seismometer. They would travel at almost constant velocity (equal to the animal's mean velocity) while the animal accelerated and decelerated. The lungs would enlarge while the animal was travelling faster than the mean and get smaller while it was slower, and they would be fullest when it had peak deceleration.

The remaining possibility is that the natural frequency of the viscera is about equal to the stride frequency. If it were tuned precisely to the stride frequency, and if the animal's pattern of acceleration and deceleration were sinusoidal, the displacements of the viscera relative to the skeleton would be in phase with the animal's fluctuating velocity. The lungs would be fullest when the animal was travelling fastest (when its acceleration

would, of course, be zero). The pattern of acceleration is unfortunately not sinusoidal, so the situation is more complicated. The animal decelerates and re-accelerates while its feet are on the ground and travels with a constant horizontal component of velocity while they are off the ground⁵. (I am ignoring a further complication: the system may be affected by vertical accelerations as well as horizontal ones.)

For the system to function as an accelerometer, the diaphragm and body wall would have to be so stiff that the amplitude of the breathing movements would be very small. For it to function as a seismometer, they would have to be so compliant that the animal would be apt to leave its guts behind in a prolonged acceleration. Neither possibility seems attractive, and neither would give the observed phase relationship between breathing and hopping. Baudinette *et al.* in their new work show¹ the lungs are emptiest while the feet are on the ground, and fullest just before the wallaby reaches the highest point in its hop.

The tuned-oscillator possibility seems to predict a reasonably realistic phase relationship and (with different degrees of damping) can give almost any amplitude of breathing movements. It seems the most likely possibility, and there is an encouraging piece of further evidence. In a study of panting, Crawford⁶ took X-ray pictures of freshly-dead dogs tilted head up and tail up. He observed how far the viscera moved between the two positions, and calculated that their natural frequency of vibration would have been about 4 Hz. This is less than the frequency of panting, which involves a different mode of vibration, but not very different from the stride frequency of about 3.2 Hz that the dogs would probably have used when running⁷.

Wallabies increase their frequency of stride very little, if at all, as they increase speed from 2 to 9 m s⁻¹ (ref. 1): they go faster by taking longer strides. Similarly, quadrupedal mammals keep their stride frequencies almost constant over their whole range of galloping speeds⁷. The concept of the respiratory system as a tuned oscillator offers a possible explanation: it would work well at the frequency it was tuned to, but not at other stride frequencies. □

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