possible relation between the pineal gland and circadian rhythms in two ways: (i) The pineal gland is necessary in sparrows for the persistence of the normal endogenous rhythms of body temperature and locomotor activity, and both sleep and body temperature changes are produced by injection of the putative pineal hormone, melatonin (*14*). (ii) The hamster pineal gland has been linked to reproductive phenomena in ways that involve day length and circadian rhythms (*15*). It is not yet possible, however, to fully relate the biochemical findings to the physiological studies. The circadian rhythm of locomotor activity of some but not all vertebrates (*16*) may be dependent on a pineal melatonin rhythm controlled by *N*-acetyltransferase activity.

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7. Thirty-six White Leghorn cockerels were obtained as day-old chicks from Thomas Mack and Sons of West Sunbury, Pennsylvania, and raised in Pittsburgh under a standard 24-hour photoperiod (lights on from 0600 to 1800 E.S.T.) with free access to food and water. The birds were housed in the topmost tiers of two adjacent cages with wire mesh covers (G.F.Q. Mfg. Co., Savannah, Georgia), each situated directly beneath a fluorescent ceiling lamp providing "cool white" illumination of approximately equivalent intensity (1380 to 1480 lu/m^2 measured at the cage tops by a Weston photometer, model 756). When 8 weeks old, the birds were decapitated in random groups of six at 4-hour intervals (0400, 0800, 1200, 1600, 2000, and 2400) during a single 24-hour period. For decapitation in the dark period, animals were exposed for 4 seconds to dim light (2 lu/m^2) from a 7.5-watt red lamp (General Electric). Following decapitation, the heads were placed immediately on ice, and the pineal glands were quickly dissected out and individually frozen on Dry Ice in coded plastic vials. The vials were shipped on Dry Ice the following day to Bethesda, where the enzyme assays were performed without prior knowledge of experimental details. After the enzyme assays, samples of the pineal homogenates were diluted and returned to Pittsburgh on Dry Ice, where they were assayed for melatonin within 3 days of decapitation. Assay methods were as follows. *N*-Acetyltransferase: N. Ellison, J. Weller, D. C. Klein, *J. Neurochem.* **19**, 1335 (1972). HIOMT: Pelham and Ralph (*5*). Melatonin: C. L. Ralph and H. J. Lynch, *Gen. Comp. Endocrinol.* **15**, 334 (1970); H. J. Lynch, in *Workshop on the Pineal Gland*, David Klein, Ed. (Raven, New York, in press).
8. Eight normal rats (average weight, 178 g) and eight normal chickens (average weight, 695 g) were decapitated. The pineal glands were dissected out, cleaned of adhering connective tissue and extracapsular vascular tissue, blotted, and weighed in the wet state. The stalks were not included. For comparison of rat and chicken enzyme values, a nocturnal *N*-acetyltransferase activity value of 3 nmole per pineal per hour was used.
9. The assays for melatonin and *N*-acetyltransferase activity were identical to those used for rats; therefore, the results obtained in chickens and rats are comparable. However, because the optimum assay conditions for rat and chicken HIOMT differ greatly, the HIOMT data are not strictly comparable. We directly compared chicken and rat pineal HIOMT activities by using the rat assay described below. In this experiment, the chicken activity was 34 times the rat activity, but the conditions were far from optimal for measuring chicken HIOMT activity. The rat microassay was modified from the method of J. Axelrod and H. Weissbach [*J. Biol. Chem.* **236**, 212 (1961)]. The reaction mixture (final volume, 20 μl) contained 0.1 m*M* *S*-[^{14}C]adenosylmethionine (52 mc/mmole) and 0.02 m*M* *N*-acetylserotonin. The final *p*H was 7.4. With both types of HIOMT assay we confirmed that some concentrations of *N*-acetylserotonin inhibit HIOMT activity in birds, as reported by B. Alexander, A. J. Dowd, A. Wolfson [*Neuroendrocinology* **6**, 236 (1970); (*5*)].
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Energy Expenditure in Animal Locomotion

Abstract. *A wide variety of data on the energy expended by animals in running, flying, or swimming can be accounted for by the simple hypothesis that all animals require the same quantity of energy to carry a unit of their own body mass one "step." For running locomotion this is approximately 3×10^{-4} calorie per gram per step.*

Schmidt-Nielsen (*1*) has reviewed a remarkable range of data on the energy which animals must consume to achieve locomotion. He defines a speed-independent consumption rate, which I will call the specific energy cost, *C*, and measure in units (*2*) of calories per gram per centimeter. This is the energy price an animal must pay to move 1 g of its own weight 1 cm. He presented the data in the form of logarithmic plots of *C* as a function of body mass (*3*). For as wide a range as six orders of magnitude in mass, the resulting plots are straight lines. Data for running, flying, and swimming are compared and show that swimming is more energetically efficient than flying, which is, in turn, more efficient than running.

A most striking feature of these data, especially when presented together as in figure 4 of (*1*), is the similarity of the slopes of the fitted lines for all three modes of locomotion. In discussing the data on running, Schmidt-Nielsen notes that they are fit by a regression line with slope -0.40, but he tenders no explanation.

I take a less statistical and more intuitive view of these plots. Using the eye as a guide, I assert that the data are fairly represented by the statement that the specific energy cost, *C*, is proportional to the inverse cube root (the

$-\frac{1}{3}$ power) of the body mass, m.

The $-\frac{1}{3}$ power dependence can be explained on the basis of a single, simple hypothesis: Energy cost per unit mass per "step" is a constant. If W is the total energy (work) required for an animal of mass m to traverse distance d, this statement becomes

$$W/m = cN = cdl^{-1} \quad (1)$$

where N is the number of steps the animal must take to cover distance d, and l is a step length or characteristic length for the animal. The energy cost per unit mass per step, c, has units of calories per gram. The characteristic length or step length is measured in centimeters and is comparable, for running, to a "mean radius" of the animal's body. Since, by definition, $W = mdC$, we may rewrite Eq. 1 in the form

$$C = cl^{-1} \quad (2)$$

It should now be noted that an animal's mass is proportional to the cube of its characteristic length. That is

$$m = kl^3 \quad (3)$$

where k is a constant which includes geometric and density information and has the dimensions of a density.

Equations 2 and 3 combined give

$$C = ck^{1/3}\, m^{-1/3} \quad (4)$$

which is in the form of our original fit of the data.

For a sphere of unit density, $k^{1/3} \approx 1.6$ g$^{1/3}$ cm^{-1}. For a man of mass 7×10^4 g whose step length is 100 cm, $k^{1/3} \approx 0.4$. If we take $k = 1$, in order to make an estimate, then from figure 4 of (*1*) we have

$$c = 3 \times 10^{-1} \text{ cal g}^{-1} \text{ (running)}$$

and similarly

$$c = 10^{-4} \text{ cal g}^{-1} \text{ (flying)}$$

$$c = 4 \times 10^{-5} \text{ cal g}^{-1} \text{ (swimming)}$$

What is the origin of the step rule? Why does a stroke cost less than a flap, which in turn costs less than a step? A plausible answer to both these questions might follow along the lines of that given by Alexander (*4*) in his discussion of the relative jumping ability of various species. His key point is that in a single contraction, muscle can do an amount of work proportional to its mass. Let us now interpret step as the unit of locomotive effort involving a single contraction of the animal's propulsive muscles. Then, insofar as the ratio of propulsive muscle mass to total body mass is a constant, the amount of energy available in a step, flap, or stroke per unit body mass is also a constant and gives the form of Eq. 4 immediately (*5*).

With regard to the relative efficiency of running, flying, and swimming, the ratio of propulsive muscle mass to body mass increases from mammals to birds, with their relatively large pectoral development, and finally to fish, where most of the body structure seems devoted to propulsion.

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2. I have chosen this somewhat less mixed set of units than calories per gram per kilometer which was used in (*1*).
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4. R. M. Alexander, *Animal Mechanics* (Univ. of Washington Press, Seattle, 1968), p. 28.
5. Another plausible argument rests on an analogy to rolling friction or friction in a bearing, as discussed in standard engineering texts [for example, S. Fairman and C. S. Cutshall, *Engineering Mechanics* (Wiley, New York, ed. 2, 1946), p. 39]. In these cases, a frictional dissipation of energy is proportional to the mass of the moving object. The analogy might be tenable in the case of running or flight, where leg or wing joints must bear the entire weight of the animal. The relevance to swimming is not immediately clear.

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Stereoscopic Vision: Cortical Limitations and a Disparity Scaling Effect

Abstract. *The spatial limitations of stereoscopic vision were studied by using vertical line stimuli containing sinusoidal disparity variations such that different parts of the line appeared at different depths. Stimuli with a finer grain than about 3 cycles per degree did not elicit depth perception, even though the sinusoidal curvature was clearly visible monocularly. At low spatial frequencies of curvature, stereoacuity was limited to the same extent as the monocular sensitivity. The limiting disparity for Panum's fusional region and the upper depth limit are subject to a scaling effect in proportion to stimulus dimensions. The disparity scaling can be characterized by a fixed maximum angular difference between the parts of the stereoscopic half-images.*

One interesting feature of stereoscopic vision is that it arises only from the combination of input from the two eyes. This combination first occurs principally at the level of the striate cortex (*1*). It is therefore possible to use stereoscopic data to study the cortical determinants of stereoscopic depth perception (*2*). The first part of this study is concerned with effects of stimulus patterning on monocular and stereoscopic acuity. Blakemore (*3*) mapped stereoacuity as a function of retinal position and disparity using conventional techniques, but he did not study stimulus configuration. Matsubayashi (*4*) found that stereoacuity was degraded as the lengths of the line stimuli used were reduced, but this was not confirmed in a recent study (*5*). Marked differences in the images to the two eyes reduce stereoacuity (*5*), but these are complex signals in terms of the dimensions of stimulus pattern.

Berry (*6*), using vertical line stimuli, studied the relation between vernier acuity and a modified stereoacuity using a vernier-type stimulus to each eye. He found that when the vertical separation of the lines was increased, vernier acuity was at first superior to stereoacuity, and then considerably degraded relative to stereoacuity, which remained essentially constant for all vertical separations. Berry considered that a "cortical interaction" may explain the results, but a simpler hypothesis is that vernier and stereoscopic processing are carried out by two systems operating relatively independently at the higher (cortical) levels. I tested this hypothesis by using vertical line stimuli containing a sinusoidal curvature or displacement, which produced static sinusoidal variations in retinal disparity when viewed binocularly.

The vertical line stimuli were generated on the face of an oscilloscope laid on its side. An oscillator fed a sinusoidal voltage of variable frequency and amplitude to the horizontal axis. The oscilloscope time base of 1 khz provided the vertical extension of the lines. Images to the two eyes were selected by the conventional arrangement of crossed polarizing filters at the oscilloscope screen and at the subject's eyes. The stimulus configuration consisted of a static sinusoidal line viewed in one eye and a straight line in the other. The lines were 15° high and 10′ thick with a luminance of 10 mlam. The subject perceived this stimulus as a line curved sinusoidally in