back is important to consider, since it might account for the apparent absence of stretch reflexes at expected latencies in human subjects reported by several investigators (*10*). The pause between a monosynaptic response to stretch and a later increase in electromyographic activity may be due to a preponderance of inhibition from Golgi organs, as has been suggested for the respiratory system (*11*). Preliminary results with standing human subjects have shown a definite inhibitory period in the electromyogram recorded from ankle extensors when these muscles are stretched by rotating a platform (*12*).

In conclusion, we demonstrate that autogenetic reflexes can compensate for variations in muscular stiffness revealed when responses to large stretches and releases are compared. Our data also show that the stiffness in response to large stretches can be greatly increased by autogenetic reflexes. The former observation supports the hypothesis that these reflexes compensate for variations in the mechanical properties of a muscle, whereas the latter supports the hypothesis that they compensate for variations in load. Our data do not allow us to distinguish which function is more important. The evidence reviewed in the preceding paragraph favors a higher gain of force feedback in normal animals. If this is true, compensation for variations in muscle properties would be greater, whereas compensation for variations in load would be less.

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Perspectives on Linear Heat Transfer

A simple linear equation relating heat flow to a temperature difference is frequently useful in describing heat exchange. Confusion exists because there are basically three different linear equations that pertain to three different situations, and the three equations are used in different ways by biologists and engineers. The origin of the difficulty seems to be a lack of agreement among biologists on a consistent set of conditions under which the particular linear equations should be applied. With a little care and more critical thought much of the confusion could be resolved (*1–3*).

Kleiber (*4*) has not helped to clarify the situation because he dealt with only two of the three linear equations and confused the substance of my earlier analysis (*1*). I think the way to gain a reasonable perspective now is to examine all three equations together, spell out their limitations, and indicate their application. The equations are:

$$dQ/dt = h_c A(T_s - T_a) \qquad (1)$$

$$dQ/dt = kA/d(T - T_a) \qquad (2)$$

$$M = C(T - T_a) \qquad (3)$$

where dQ/dt is the total rate of heat flow; h_c is the convective surface conductance; k is the thermal conductivity; A is the heat transfer area; d is the thickness over which a temperature gradient exists; T_s, T, and T_a are, respectively, surface temperature, "bulk" core or body temperature, and ambient temperature; M is the metabolic heat production rate; and C is a coefficient.

Equation 1 is called, in modern engineering heat transfer, Newton's law of cooling (*5*) and Newtonian cooling (*6*). It is used to describe convective heat flow. In heat convection the boundary layer heat flux (from the surface of an object to the surroundings) is described by a set of partial differential equations. For mathematical simplicity, Eq. 1 is often assumed, instead, to adequately describe this heat flux. It is generally agreed that the equation is not a phenomenological law of heat convection but rather a definition of h_c. Equation 1, as it stands, does not describe cooling of an object but rather the heat transfer from its surface to the environment. To describe cooling, one must equate this to the time rate of change of internal energy of the object, whereupon the solution for T as a function of time yields the cooling equation (*1, 6*). For Eq. 1 to describe the loss or gain of heat by the entire object, the object must have a very large thermal conductivity so that only very tiny thermal gradients occur within it (the "bulk" temperature of the object and its surface temperature are then virtually equal), and the time-temperature history is controlled by the surface resistance, to which Eq. 1 applies. This is called Newtonian heating or cooling because the object is now similar to the red-hot block that Newton used in his experiments. I suggested (*1*) the following origin for Eq. 1: Use Newton's original proportionality (determined under the simultaneous conditions of conduction, convection, and radiation)

$$d(T_s - T_a)/dt \propto (T_s - T_a) \qquad (4)$$

and the first law of thermodynamics for a closed system

$$dQ = dH - VdP$$

(**H**, **V**, and **P** are, respectively, enthalpy, volume, and pressure). Then, after the time derivative of the first law at constant **P** is taken,

$$dQ/dt = C_p dT/dt$$

(C_p is the total heat capacity of the system) substitution of Newton's proportionality for dT/dt would, with a few assumptions, lead to Eq. 1, the total heat exchange between the system and the surroundings across the system's surface area A. I called this the contemporary Newtonian law of cooling to distinguish it from Eq. 4 and relate it to modern engineering usage. My choice of semantics may have caused Kleiber (*4*) to think I tried to develop some "new Newtonian cooling law," which he argued is confusing. Actually, I showed that Newton's original proportionality (which dealt with temperature, not heat) plus the first law of thermodynamics (which does deal with heat) could together yield a heat flow equation independently of Fourier's law. The rigid conditions under which this is possible have been discussed elsewhere (*1*), as well as another approach to Eq. 1 that does not use Newton's proportionality but uses, instead, a "Newtonian" object (extremely large k) and applies Fourier's law to the stagnant film next to the object.

Equation 2, integrated over time, was called by Hardy (*7*) a "law of steady-state heat conduction," and indeed it is. It is a steady-state ($dT/dt = 0$) integration of Fourier's law, $\mathbf{q} = -k\nabla T$, where $\mathbf{q}$ is the heat flux vector:

$$dQ/dt = \int_A \mathbf{q} \cdot d\mathbf{A} = -\int_A k\nabla T \cdot d\mathbf{A} \quad (5)$$

If k is not a function of ∇T, ∇T is not a function of time, and $\nabla T \cdot \mathbf{n} = -(T - T_a)/d$ is a good approximation ($\mathbf{n}$ is the unit outward normal vector); then

$$dQ/dt = kA/d(T - T_a)$$

where k is the average thermal conductivity of whatever material supports ∇T. Equation 2 applies only to heat conduction in the steady state, despite the fact that it appears similar to Eq. 1, and this has been a source of confusion [for example, see (*8*)]. While k is a property only of the material (gas, liquid, skin, fur, and so forth) and possibly a function of its temperature, h_c in Eq. 1 reflects not only surface properties of the object but also properties of the surroundings (velocity, density, viscosity, and so forth).

Equation 3 has found special preference among biologists but was not discussed by Kleiber (*4*). It is probably the most misunderstood equation in thermoregulation, where it has been confused with Eq. 1, and Fourier's law and repeatedly used with little regard for its limitations. It states that the rate of internal heat production (metabolism, M) is a linear function of the difference between body temperature and ambient temperature. The coefficient C is called a conductance; it is determined from a graph of the oxygen consumption rate of an animal (which is related to heat production) against ambient temperature and used to compare the thermoregulatory responses of a wide variety of animals in order to see evolutionary and ecological adaptations. Biologists call it Newton's law of cooling, and we see another source of confusion. The only similarity between Eq. 3 and Newton's experiments or engineering heat transfer is that something, M, is a linear function of a ΔT. The expression actually comes from the general heat equation, where locally,

$$\rho c_p dT/dt = -K\nabla^2 T - dQ'/dt \quad (6)$$

where ρ is the density and c_p the specific heat capacity. The left side of Eq. 6 is the local (per unit volume) time rate of change of internal energy, and the first term on the right is the net rate at which heat is being transported away from the local point whose temperature is T. The local rate of heat production is dQ'/dt. Many assumptions are required to develop a linear relation between dQ'/dt and $(T - T_a)$, particularly in a nonlocal form and for an insulated animal experiencing convective surface heat exchange. But in proceeding by this route the important variables and conditions can produce a coefficient C that is a well-defined function of these variables (*1, 2*). As normally determined, C is a lumped conductance and contains not only the conductance of skin, fur, or feathers but also the convective surface conductance, h_c, itself a function of environmental variables (*1, 2*). Therefore, C cannot reflect solely properties of the animal, unless the environment in which it is measured is rigidly and precisely recreated for each measurement. The alleged linearity of Eq. 3 has also been questioned (*9*).

If we must call one of the three equations Newton's law, then I think it best to reserve the label for Eq. 1 because it is the only one of the three whose origin could include Newton's original proportionality, and the only one that applies to conditions similar to those of Newton's experiments. Equation 2 is an integration of Fourier's law and applies only to steady-state heat conduction. Equation 3 must come from the general heat equation, will hold only under specific conditions, is not really related to anything Newtonian, and contains, as it stands, a poorly defined and certainly variable coefficient, C. None of the three equations describe cooling. One must distinguish among the modes of heat transfer and apply the appropriate equations to them.

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Kleiber (*1*) has stated that "several physiologists confuse Fourier's law of animal heat flow with Newton's law of cooling." This can be an important message to those who confuse the processes and mechanisms of cooling with those of heat transfer. However, the equations most often used by physiologists to describe heat transfer from homeotherms are neither Newton's law of cooling nor Fourier's law of conductive heat transfer (although they are based on these laws). The physiological equations usually have the form:

$$M = C(T_b - T_a) \quad (1)$$

where M is the metabolic rate of the homeotherm, C is often called the thermal conductance, T_b is the core body temperature, and T_a is the ambient air temperature (*2*). However, C is often given units that are related to heat production but have nothing to do with heat transfer or cooling (such as milliliters of oxygen per hour per degree). Furthermore, since these equations usually implicate air temperature in their driving functions (when the equations are used to describe animal heat flow) they cannot be equivalent to Fourier's rate equation for heat conduction, because the mechanisms of heat transfer from homeotherms to the environment include convection and radiation as well as conduction (*2, 3*).

The fact that Eq. 1 can be fit closely to data on the metabolic rates of most homeotherms implies that it can be regarded as an appropriate regression model of a homeotherm's metabolic response to the exact environments in which the data were obtained. However, Tracy (*4*) has warned that the physical environment in which metabolic data are taken interacts complexly with the size and shape of the organisms (for example, small animals are influenced more by wind, in terms of convective heat transfer, than large animals). Thus, the regression model (Eq. 1) may not be an appropriate tool for comparing metabolic responses of different species of homeotherms (or even different-sized homeotherms of the same species), and it is certainly inappropriate as a predictive model of the metabolic responses of homeotherms in natural environments (*4*).

Kleiber has applied "an especially simple form of Fourier's law to the heat flow in the body of homeothermic animals schematized as a core with a constant temperature T_b surrounded by an insulating layer with heat conductivity λ, thickness L, surface area S, and surface temperature T_s" [(*1*); see also (*5*)]:

$$\frac{dQ}{dt} = \lambda \frac{S}{L} (T_b - T_s) \qquad (2)$$

where dQ/dt is the instantaneous heat flow from the animal. Kleiber also noted that Eq. 2 is used by architects and engineers to calculate the heat conducted from houses, but its use in physiological publications has been rare (*1*). Actually, Eq. 2 is a special case of Fourier's equation (*6*) that is well suited for calculations of heat transfer through flat slabs (such as the walls of houses), but possibly inappropriate for descriptions of heat transfer from animals. For example, heat transfer through a flat slab is conducted through the same cross-sectional area throughout the thickness of the slab, but heat transfer from a roughly cylindrical animal is transferred from a core, with a definable surface area, to the outer surface of the insulating "shell," where the surface area is relatively larger. Therefore, heat flow through the insulating layer of animals is not linear with respect to position in the insulating layer, as suggested by Kleiber's approximation (Eq. 2) of the Fourier equation.

For the sake of semantic clarity, historical truth, and mechanistic accuracy, Kleiber's distinctions between Fourier's law and Newton's law are very important. However, it is perhaps even more important for biologists to know the limitations of the equations they have for so long called Newton's or Fourier's law (*4, 7*).

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3. When air temperature is the only environmental variable in the driving function of these equations, it is implicitly assumed that the thermal radiative environment and the environment implicated in conductive heat transfer from the animal are at the same temperature as air. This assumption may be in error by as much as 30°C under natural conditions. Evaporative heat loss cannot be properly accounted for in Eq. 1, because the driving function for evaporative heat loss must include relative humidity as well as environmental temperature.
4. C. R. Tracy, *BioScience* **22**, 656 (1972).
5. M. Kleiber, *Hilgardia* **6**, 323 (1932); *The Fire of Life* (Wiley, New York, 1961).
6. Fourier's law is $dQ/dt = -kA(dT/dx)$, where dQ/dt is the instantaneous heat flux across the area A, k is the thermal conductivity, and dT/dx is the temperature gradient at A [see J. P. Holman, *Heat Transfer* (McGraw-Hill, New York, 1968), p. 2].
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I appreciate Tracy's recognition and am sorry that Strunk finds that my report has not helped to clarify the situation. He blames me for not discussing the equation $M = C(T - T_a)$, which states that the metabolic rate of animals is proportional to the difference between body temperature and ambient temperature. Newton's law deals with temperature loss and Fourier's law with heat flow; neither expresses metabolic rate and I was justified in avoiding an unnecessary complication in my report. Since both commentators brought up the metabolic rate, I can add that the equation above applies to homeotherms only in an ambient temperature below the lower critical temperature, when the metabolic rate changes as a part of "chemical temperature regulation" (*1*). When the ambient temperature rises to the thermoneutral zone the metabolic rate becomes independent of changes in ambient temperature. I have discussed this special problem elsewhere (*2*).

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Serious Contaminant in "Ultra Pure" Grades of Sucrose

In the course of our studies we have discovered that several lots of the "Ultra Pure enzyme-grade" (Nos. X3822 and X3233) and "RNAse-free grade" sucrose (No. X3927) supplied by Schwarz/Mann contains a contaminant that may preclude its use in certain density gradient applications. When subcellular particles such as polyribosomes are purified by zonal centrifugation on gradients prepared with this sucrose, and then RNA is extracted from the particles by a conventional procedure such as that in which sodium dodecyl sulfate, chloroform, and phenol are used, the contaminant is isolated together with the RNA. The contaminant, which is insoluble in 70 percent ethanol, is also relatively insoluble at the low salt concentrations ($\leq 0.1M$) normally used to dissolve RNA, producing a slight turbidity which can interfere with ultraviolet absorption measurements. An even more serious consequence of the contaminant is that its presence in RNA preparations causes an appreciable amount of nonspecific binding of the RNA to both Millipore and polyuridylic acid–impregnated glass fiber filters which are now commonly used in assays of RNA containing polyadenylic acid. Fortunately, the contaminant is readily soluble in $1M$ NaCl, and, thus, if one washes the RNA precipitates with $1M$ NaCl before dissolving them in the low salt solution, one can eliminate the contaminant, and obtain RNA that gives reliable results with the Millipore or polyuridylic acid–glass fiber filter binding assays. Of course, there is an unavoidable loss of low-molecular-weight RNA by this procedure.

The contaminant was not found in the grade 1, crystalline sucrose supplied by another company. Its presence in any particular sample of sucrose can be demonstrated by adding an equal volume of ethanol to a 45 percent solution of the sucrose. The solution, after standing at room temperature, will exhibit readily visible turbidity within 15 minutes if the contaminant is present.

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Schwarz/Mann offers Ultra Pure Sucrose, No. 90-9530, as a special grade, free of ribonuclease activity, for sucrose density gradient centrifugation of RNA preparations. Our assay procedure for ribonuclease calls for 18 hours of incubation with RNA at 37°C and