

thus placed 3 mm apart in a plane orthogonal to the muscle fibers at depths of 26 mm (No. 1), 23 mm (No. 2), and 20 mm (No. 3). Appropriate connections gave the subject both audio and visual feedback from the middle electrode (No. 2) via a loudspeaker and monitor oscilloscope. Activity from all three electrodes was observed by the experimenter and recorded on magnetic tape.

The subject was instructed to select a single motor unit from among those registered from electrode No. 2 and to isolate this unit. Once he isolated a unit, he was asked to demonstrate control of it by varying its rate of discharge and then by repeating simple three-beat rhythms. Upon achieving these criteria, the subject was asked to isolate and train a second, and then a third, motor unit in the same manner. The FM tape recording from all electrodes provided permanent records for later analysis.

Although there was considerable variation, all subjects met the usual criteria of control for at least one single motor unit. During the course of selecting, isolating, and controlling the unit on electrode No. 2, three different patterns of response were recorded from the adjacent electrodes (Nos. 1 and 3): (i) random firing of neighboring motor units, (ii) electrical silence, and (iii) cross talk from the unit being trained. (Cross talk was identified by establishing a strict one-to-one correspondence between frequency of the unit being trained and that of the activity recorded from electrode Nos. 1 or 3.) As a rule, random firing of neighboring units recorded from electrode Nos. 1 and 3 decreased as the subject gained more precise control of the trained unit. When there was a high degree of control over a trained unit on No. 2 (ability to vary the rate easily without breakthrough of unwanted units), electrical silence on electrode Nos. 1 and 3 was shown in four of five subjects.

In the one subject for whom this silence was not found, random activity

on electrode Nos. 1 and 3 decreased markedly as she achieved more control over the unit on No. 2. An exception to this relationship between control of a unit and silence of its neighbors occurred when subjects attempted to produce three-beat rhythms. Often there was a short burst of activity on electrode Nos. 1 and 3 as the subject initially attempted to discharge a trained unit in No. 2 with the designated cadence. Also, even when the unit was well controlled, firing it at high frequency was generally associated with some activity on electrode Nos. 1 and 3.

We conclude that as a single motor unit in the biceps brachii is trained with biofeedback techniques, the neighboring motor units show a progressive tendency toward electrical silence, even though the subject has no artificial feedback from them. This demonstrates the natural progressive inhibition of surrounding portions of the muscle in which a single unit is being selectively trained. This inhibition is similar to what occurs in surrounding muscles (2). These results suggest that the individual members of a motoneuronal pool can be selectively activated without activation of immediate neighbors in the same pool.

H. MCCORD SMITH, JR.

JOHN V. BASMAJIAN

SANDRA F. VANDERSTOEP*

Regional Rehabilitation Research and Training Center, Emory University, and Georgia Mental Health Institute, Atlanta 30306

References and Notes

1. J. V. Basmajian, *Science* **141**, 440 (1963); J. H. Petajan and B. A. Philip, *Electroencephalogr. Clin. Neurophysiol.* **27**, 66 (1969); J. V. Basmajian, *Science* **176**, 603 (1972).
2. J. V. Basmajian and T. G. Simard, *Am. J. Phys. Med.* **46**, 1427 (1967).
3. J. V. Basmajian, *Muscles Alive: Their Functions Revealed by Electromyography* (Williams & Wilkins, Baltimore, ed. 3, 1974), pp. 114-120.
4. Supported by a summer scholarship to H.McC.S. from the Social and Rehabilitation Service, Department of Health, Education, and Welfare.
- * Visiting scientist from State University College at Brockport, New York.

9 October 1973; revised 16 November 1973 ■

Linearized Heat Transfer Relations in Biology

Kleiber (1, 2), Strunk (3), and Tracy (4) have commented on the nomenclature, uses, and misuses of various linear heat transfer relations in biology, with particular reference to Newton's "law" of cooling and Fourier's law of conduc-

tion. These papers reflect the increasing realization within the biological community that the problems of thermoregulatory physiology and ecology are best approached with the proper use of heat transfer relations developed in

physics and engineering. Human physiologists have used this approach for some time (5), and more recently heat transfer theory has been applied to more general problems in botany and zoology (6, 7).

The recent papers (1-4) in *Science* are a positive contribution in calling some of this work to the attention of a wider audience. However, we consider that Kleiber (1, 2) and Strunk (3) have added to the confusion in the use of the various heat transfer relations.

First, Strunk neglects radiative heat transfer. His equation 1

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

gives the rate of heat transfer dQ/dt from an animal of area A and surface temperature T_s to an "ambient" temperature T_a (apparently air temperature), where h_c is the "convective surface conductance" [apparently (7) the convection coefficient]. However, heat is also transferred to and from an animal by thermal radiation, and often conduction to the substrate is significant. Total heat transfer can be expressed in the simple form of Eq. 1 only if substrate conduction is negligible; h_c is replaced by the overall heat transfer coefficient $h = h_c + h_r$, where h_r is the linearized radiation coefficient; and the radiative temperature of the environment T_r is equal to air temperature T_a . Even with these corrections, Eq. 1 only approximates dQ/dt since radiative heat transfer is nonlinear. The Stefan-Boltzmann law for radiative heat transfer in a uniform radiative environment

$$dQ_r/dt = F\sigma A (T_s^4 - T_r^4) \quad (2)$$

depends on the fourth power of the temperatures; σ is the Stefan-Boltzmann constant, and F is a factor to correct for shape and surface emissivities less than 1 (8, pp. 216-229). Equation 2 may be approximated by a linear relation (8, p. 230), but is accurate only for small (10° to 20°K) temperature differences $T_s - T_r$.

Radiative heat transfer is not negligible relative to convective heat transfer, as may be seen by approximating an animal by a black cylinder in a black cavity with $T_r = T_a$ and comparing h_c with h_r . For typical cases, radiation accounts for 15 to 80 percent of the total heat transfer, even when published values (8, p. 411) for the convection coefficient are increased by 50 percent to include turbulence effects (8, p. 412; 9). We comment on Strunk's (3, 7) work in more detail elsewhere (10).

Strunk (3) and Kleiber (1), respectively, have referred to Eq. 1 as Newton's law or Fourier's law. Neither designation is satisfactory or consistent with historical or current usage.

Most authors credit Newton with proposing a linearized relation for convective or radiative heat transfer, or both, but usually do not designate it as Newton's law of cooling. They differ in regarding Newton as having proposed a linearized convection (11, 12), radiation (13), or overall (convection plus radiation) (14) coefficient. Some authors make use of a linearized overall heat transfer coefficient equation similar to Eq. 1 but make no mention of Newton (15). This lack of unanimity, together with the problems associated with the use of the term Newton's law in the biological literature, makes any use of this term confusing, and it should be abandoned.

As Tracy (4) noted, the term Fourier's law is used exclusively in contemporary texts (11, 15) to designate the fundamental law of conductive heat transfer. Kleiber (1) has noted this difference and has suggested that the term Fourier's law be expanded to include all avenues of heat loss (convection and radiation as well as conduction). As well as being inconsistent with current usage in heat transfer, this would be historically inaccurate. Fourier (16) indicated that his theory could not be applied to convective heat transfer (16, p. 462) and that convection and radiation were complex and nonlinear (16, pp. 30, 31, 43, and 465). The study of convection and radiation has been the work of many physicists and engineers and has followed Fourier's work with conduction.

We suggest that Kleiber's original concern, identifying Eq. 1, would be resolved by abandoning the use of the term Newton's law and reserving the term Fourier's law for conduction. The convenient linear approximation to heat transfer of Eq. 1 would best be designated as "the linear approximation to overall heat transfer" and the coefficient designated as the "overall heat transfer coefficient." Alternatively, the designation "electrical analog of heat flow," commonly used in heat transfer texts and consistent with Kleiber's (1) remark on the analogy between Eq. 1 and Ohm's law in electricity, could be used.

The study of heat transfer in animals is inherently interdisciplinary, involving physiology, heat transfer physics, and meteorology, and we feel that it is

very important to maintain consistent usage of terms.

We wish to emphasize that Eq. 1 is a convenient approximation, and not in any sense a law, as has been known for 150 years (16). Heat transfer in animals, especially outdoors, is extremely complex, involving conduction, convection, radiation, and mass transport with phase change. Any approximation such as Eq. 1 must be used with full awareness of the limits to its validity and the actual factors contributing to the heat flow. Workers in this field should be familiar with heat transfer theory through basic texts [for example (8)] and texts and papers applying this theory to animals correctly [for example (5, 6)].

G. S. BAKKEN

D. M. GATES

Department of Botany, University of Michigan, Ann Arbor 48104

References and Notes

1. M. Kleiber, *Science* **178**, 1283 (1972).
2. ———, *ibid.* **181**, 186 (1973).
3. T. H. Strunk, *ibid.*, p. 184.
4. C. R. Tracy, *ibid.*, p. 185.
5. D. M. Kerslake, *The Stress of Hot Environments* (Cambridge Univ. Press, London, 1972), or other recent texts in human thermal physiology.
6. D. M. Gates, *Energy Exchange in the Biosphere* (Harper & Row, New York, 1962); R. C. Birkebak, *Int. Rev. Gen. Exp. Zool.* **2**, 269 (1966); W. P. Porter and D. M. Gates, *Ecol. Monogr.* **39**, 227 (1969); C. R. Tracy, *BioScience* **22**, 656 (1972).
7. T. H. Strunk, *J. Theor. Biol.* **33**, 35 (1971).
8. F. Kreith, *Principles of Heat Transfer* (International Textbook, Scranton, Pa., ed. 2, 1965).
9. G. I. Pearman, H. L. Weaver, C. B. Tanner, *Agric. Meteorol.* **10**, 83 (1972).
10. G. S. Bakken and D. M. Gates, *J. Theor. Biol.*, in press.
11. A. J. Chapman, *Heat Transfer* (Macmillan, New York, 1960), pp. 5 and 12; M. Jakob, *Heat Transfer* (Wiley, New York, 1949), vol. 1, p. 2.
12. Although cited by Strunk (3), Kreith (8, pp. 9 and 14) does not use the term "Newton's law of cooling."
13. J. M. Cork, *Heat* (Wiley, New York, ed. 2, 1942), p. 159.
14. E. R. G. Eckert, *Heat and Mass Transfer*, J. F. Gross, Transl. (McGraw-Hill, New York, 1963), pp. 5, 17, and 18; A. J. Ede, *An Introduction to Heat Transfer Principles and Calculations* (Pergamon, Oxford, 1967), pp. 7, and 40-41.
15. W. M. Kays, *Convective Heat and Mass Transfer* (McGraw-Hill, New York, 1966), pp. 2 and 13; W. M. Rohsenow and H. Y. Choi, *Heat, Mass, and Momentum Transfer* (Prentice-Hall, Englewood Cliffs, N.J., 1961), pp. 5 and 88.
16. J. B. J. Fourier, *The Analytical Theory of Heat* (1822; translation by A. Freeman, 1878; reprinted by Dover, New York, 1955).
17. Supported by the Ford Foundation and by grant AEC-AT(11-1)-2164 from the Atomic Energy Commission.

20 August 1973; revised 15 October 1973

Bakken and Gates have observed that my comment (1) dealing with linear heat transfer neglected the nonlinearities of radiation heat exchange. I explicitly did this originally (2, p. 37) and continued to do so (1) because there was no significant confu-

sion of radiation with other modes of heat flow or of the nonlinear Stefan-Boltzmann equation with the linear equations I discussed, and not because I thought it an unimportant avenue of heat exchange. It should be realized, as they point out, that radiation must be accounted for in a complete description of heat transfer. Despite Bakken and Gates's contention, I do not think my approach generated more confusion than it avoided. On the contrary, there existed sufficient misunderstanding in the biological literature over the terminology and equations of heat conduction, convection, and generation without an analysis encumbered with the nonlinearities inherent in radiation heat transfer.

No one could argue with their statement on the importance of radiation. But the four *Science* papers Bakken and Gates refer to were dealing with common linearizations and not with cases where the linearization of the Stefan-Boltzmann equation might apply. For simultaneous conduction, convection, and radiation, an overall equation might not be amenable to solution in closed form because of the complex nature of the coefficient h .

Bakken and Gates remark that my designation (1) of Eq. 1 above as Newton's law is neither satisfactory nor consistent with historical usage, but they give no substantial argument to support this. I did not call Eq. 1 Newton's law, but said that in modern engineering heat transfer it was called either that or Newtonian cooling. I called it a "contemporary" Newtonian law of cooling to distinguish it from Newton's original proportionality, and suggested that if we must call one of the linear equations Newton's law of cooling, then Eq. 1 is the proper candidate. I have explained in detail (1) why I think this is most satisfactory and have discussed at length (2) why it is historically most consistent.

A point often missed is that Newton was actually measuring temperatures, not heat flow or content, and his original proportionality was between the rate of temperature change and the temperature difference between the hot iron block and the surroundings. To "credit Newton with proposing a linearized relation for convective or radiative heat transfer, or both" is misplacing credit and is historically wrong, for it was not until 60 years later that the distinction between heat and temperature was made.

The overall lack of unanimity on the origin or application of Newton's work is not sufficient reason to stop referring to anything in heat transfer as "Newtonian." I chose instead to analyze the origin, limitations, use, and context of Newtonian heat exchange (through an admittedly expository device called a Newtonian animal) (2). This allows Newton's observations to be combined with the first law of thermodynamics and a well-defined set of conditions that, together, will produce a linear heat flow equation, Eq. 1. Thus, we can place Newton's work in historical and scientific context and are probably pretty close to the way the equation actually evolved. In the context of Bakken and Gates's comments it is not possible to explain how Newton's observations on temperature might have found their way into heat transfer theory.

I concur with Bakken and Gates's paragraph on Fourier's law, and before Tracy's comment (3) I had specifically described the limitations and use of not only Fourier's law but also Fourier's equation and a number of other equations common in heat transfer and urged a usage in biological systems consistent with that in heat transfer theory (2).

I do not see the advantage of terming Eq. 1 "the linear approximation to overall heat transfer." The coefficient h will be a complicated function of many variables, and the applicability of the equation will be limited to the range of validity of the linearization. I think the alternative, the "electrical analog of heat flow," obscures the historical and thermodynamic relationships that place the equation in a framework that includes the constraints.

The constraints that exist in various situations must be defined before consistency will replace confusion. My suggestions were derived from system constraints and their connection to history. I think it is the more coherent alternative.

There is a correction to Bakken and Gates's reference 12. Kreith lists "Newton's law of cooling" in his index (p. 616) and assigns its occurrence to p. 14, where a very familiar equation appears.

THOMAS H. STRUNK*

109 Columbia Street,
Brookline, Massachusetts 02146

References and Notes

1. T. H. Strunk, *Science* **181**, 184 (1973).
2. ———, *J. Theor. Biol.* **33**, 35 (1971).
3. C. R. Tracy, *Science* **181**, 185 (1973).
- * Present address: Electron Probe Resource, Laboratory of Human Reproduction and Reproductive Biology, Harvard Medical School, Boston, Massachusetts 02115.

10 December 1973

It is encouraging to find that the discussions in *Science* started in 1972 (1) have clarified several ideas concerning heat transfer in organisms. Among these are: (i) Newton's law of cooling is a law of temperature loss, not of heat flow. Heat flow is a concept of post-Newtonian caloric theory (which survived the riddance of the erroneous posit that heat is a material substance). (ii) Newton's law of cooling is limited to bodies without internal heating; therefore it cannot apply to living organisms, one of whose essential characteristics is metabolism, which involves internal heat production. (iii) The claim that Fourier supported the application of Newton's law of cooling to heat flow loses significance since the publication of the long-lost 1807 version of Fourier's *Analytical Theory of Heat* in 1972 (2). This book contains information which indicates that Fourier was somewhat confused about Newton's work on heat (2, p. 273, footnote). (iv) Fourier's law of heat conduction excludes convection. Bakken and Gates cite Fourier's own judgment on that question. This, unlike his notion of Newton's work on heat flow, is compelling.

When I extended Fourier's law from conduction alone to total heat flow I changed "conductivity" to "transfer-

bility" and "conductance" to its reciprocal "resistance to heat flow" in order to avoid confusion. Keeping Fourier's name for this extension was a semantic error because two Fourier laws of heat transfer could be a source of confusion. The criticism of Bakken and Gates is therefore justified. I will follow their recommendation and change my terminology from the "extended Fourier law" to the "linear approximation of total heat flow."

MAX KLEIBER

Department of Animal Science,
University of California, Davis 95616

References

1. M. Kleiber, *Science* **178**, 1283 (1972).
2. J. B. J. Fourier, *The Analytical Theory of Heat* (MIT Press, Cambridge, Mass., 1972), p. 273.

10 January 1974

Sex Pheromone of the Codling Moth

(2Z,6E)-7-Methyl-3-propyl-2,6-decadien-1-ol, proposed by McDonough *et al.* (1) to be a sex pheromone of the codling moth, *Laspeyresia pomonella* (L.), was found to be unattractive. (E,E)-8,10-Dodecadien-1-ol, discovered by Roelofs *et al.* (2) to be a sex attractant as determined by the electroantennogram method, was found in our laboratory, by physical data and ozonolysis, to be the authentic natural sex pheromone.

L. M. McDONOUGH

H. R. MOFFITT

Yakima Agricultural Research
Laboratory, Agricultural Research
Service, U.S. Department of
Agriculture, Yakima, Washington

References

1. L. M. McDonough, D. A. George, B. A. Butt, J. M. Ruth, K. R. Hill, *Science* **177**, 177 (1972).
2. W. E. Roelofs, A. Comeau, A. Hill, G. Milicevic, *ibid.* **174**, 297 (1971).

26 December 1973