muscle and temperature

Introduction: Influence of temperature on muscle and locomotor performance

Temperature has a large influence on many physiological functions including muscle contraction. Temperature's effect on muscle contraction has attracted the attention of a wide range of scientists, from molecular biologists to ecologists, who have studied the influence of temperature on muscle for very different reasons. Because temperature has a larger effect on some muscle properties than others, biophysicists and cell physiologists have traditionally used temperature changes as an experimental perturbation to determine which particular step in the complex process of contraction is rate limiting. Because temperature is also an important environmental variable, integrative physiologists and ecologists have used temperature changes to assess the influence of temperature on whole animal performance, to determine the mechanisms used to compensate for changes in temperatures, and finally to determine adaptation to the thermal environment in which animals live. Although these viewpoints and approaches are distinct, many individuals who use temperature as an experimental perturbation become interested in the behavior of animals at different temperatures. Similarly, those interested in ecological implications of temperature become interested in the underlying molecular mechanisms for these limitations. This crossover of interest makes the influence of temperature on muscle a fascinating subject and has enabled us to attract biophysicists, cell physiologists, integrative physiologists, ecologists, and molecular biologists to participate in our symposium entitled "Influence of temperature on muscle and locomotor performance." This symposium was held in two parts: one at the 1989 Federation of American Societies of Experimental Biology meeting in New Orleans, LA, and the second at the 1989 International Union of Physiological Sciences meeting in Helsinki, Finland. The series of papers that follow is a compilation of articles from both sessions.

A number of important conclusions came out of the symposium. Rall and Woledge (8) showed that some muscle properties have large thermal dependencies while others have small ones. Most importantly, they showed that the thermal dependence of some muscle properties can be complex. In the case of muscle relaxation, for instance, there are two factors working in parallel with differing Q_{10}[1] values. Because one of these factors is saturable, the Q_{10} for muscle relaxation depends on duration of muscle activity. Stevens and Godt (10) discussed another complexity, the concomitant change in pH when temperature changes in vivo. They demonstrated that the compensatory effects of the pH change tend to reduce the pure temperature effect. In particular, an increase in calcium sensitivity at low temperatures may decrease the cost of contraction (10).

The largest change in muscle mechanics with temperature is the reduction in maximum velocity (V_{max}) of shortening and mechanical power generation at low temperatures. Despite this reduction, Rome (9) showed that animals must generate the same power and force to locomote at a given speed at low temperatures as they do at high ones. They do this by recruiting more muscle fibers at the low temperature than at the high ones ("compression of the recruitment order"), enabling the animals to locomote in precisely the same fashion at a given speed irrespective of temperature. This neural mechanism is one of many that animals must use to deal with temperature changes. Montgomery and Macdonald (7) demonstrated that, although temperature changes can dramatically alter the individual functional parameters of the nervous system, the final outcome (efferent output and behavior) is often far less affected. This is because of internal temperature compensation mechanisms, in which temperature changes have opposing effects on individual parameters.

Although animals can still operate over a wide range of temperatures, Rome (9) and Bennett (1) showed that in some forms of locomotion (jumping and swimming) maximum performance and maximum sustainable performance are greatly influenced by temperature, primarily through its effect on V_{max} and maximum power generation. In some other types of locomotion such as running, however, Marsh (6) has shown that contractile kinetics may determine cycling frequency and hence determine maximum speed, particularly at low temperatures. The influence of temperature on muscle deactivation may be the primary determinant of contractile frequency, and this effect on frequency may in turn set the limits of locomotor power and speed.

Faced with the problem of reduced maximum and maximum sustainable performance at low temperatures, some fish acclimate. Acclimation enables some fish to increase locomotor performance in the cold (3, 5, 9). This compensation is primarily due to an increase in V_{max} and power output of the muscle (5). Johnston et al. (5) provided evidence that the increase in V_{max} associated with thermal acclimation is due to different myosin light chains expressed during cold acclimation. Alternatively, Gerlach et al. (3) provided molecular biological evidence

[1] Throughout these symposium papers, the temperature dependence of a process is represented by a temperature coefficient or Q_{10}. $Q_{10} = (R_2/R_1)^{[10/(T_2-T_1)]}$, in which R_2 and R_1 are rate processes or quantities at temperatures T_2 and T_1, respectively, and $T_2 > T_1$.

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that the increase in V_{max} may be due to the expression of different myosin heavy chains at different temperatures.

In addition to the contractile apparatus, the metabolic machinery also undergoes thermal acclimation. Guderley (4) reported that when fish are acclimated to a temperature more than 8°C below their optimum for locomotor performance, compensatory increases of muscle aerobic capacity occur. While cold-active fish probably exploit this increase, cold-inactive fish use this machinery to aid alternative metabolic strategies. She also found that other aspects of life history besides temperature may have a significant effect on these changes.

Although some fish have the ability to acclimate, Bennett (1) pointed out that acclimation is always incomplete and in most animals is entirely absent. He found that locomotor performance in different groups possess the attributes (e.g., variability, repeatability, heritability, and differential survivorship) necessary for evolutionary adaptation and that partial (but incomplete) adaptation to environmental temperature can occur.

Although most of the discussion at the symposium focused on ectothermal animals, Faulkner and colleagues (2) showed that the muscles of mammals can undergo significant temperature changes and their muscles are influenced by temperature in a similar manner to that of ectotherms. Thus, faced with the same problems, mammals resort to the same basic mechanism of recruiting more motor units at low temperatures to sustain a given level of power.

As well as revealing many new generalizations concerning muscle and locomotor performance, the symposium revealed new directions for future research. Comparative and integrative muscle physiology is a field that is just beginning to flower, particularly in its molecular and organismal aspects. Studies of the effects of such variables as temperature have shown much promise in permitting physiologists of many disciplines to interact fruitfully and to investigate problems over a wide range of functional levels. We anticipate considerable new insight to come forth in these areas in the next few years.

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Address for reprint requests: L. C. Rome, Dept. of Biology, University of Pennsylvania, Philadelphia, PA 19104.

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Lawrence C. Rome
University of Pennsylvania, Philadelphia

Albert F. Bennett
University of California, Irvine

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