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FRONT MATTER: DISCOVERY

Why is it easier to run in the cold?

Comment on: Yoo Y, LaPradd M, Kline H, Zaretskaia MV, Behrouzvaziri A, Rusyniak DE, Molkov YI, Zaretsky DV. Exercise activates compensatory thermoregulatory reaction in rats: A modeling study. J Appl Physiol (1985) 2015; 119:1400-10; PMID: 26472864; http://dx.doi.org/10.1152/japplphysiol.00392.2015

Overheating is one of the main factors limiting physical activity. During running, thermoregulatory metabolism, which keeps core temperature steady at rest, is adjusted through a body temperature independent mechanism to compensate for the exertional heat generation. The colder the environment, the higher the metabolism at rest, and the more complete the compensation is.

As a marathoner, one of us logged many miles of training which serve as an interesting dataset spanning several summer and winter seasons. Strikingly, the average pace during the winter months appears to be about 1 minute per mile faster than during the summer months, displaying a huge difference in performance. Besides, every long distance runner knows that it may take a noticeably longer time to start sweating when it is cold outside in spite of an often faster pace and warmer clothing. This raises the question why colder environment possibly leads to a slower temperature growth and to a potentially better performance.

High body temperature is a major regulatory signal to limit the physical effort and, thus, to prevent the temperature from growing further. So, for the effort to remain at high level, the temperature should stay away from this threshold for as long as possible. The rate of temperature change is defined by a balance between 2 processes: heat produced vs. heat dissipated per unit of time. Importantly, both heat production and skin thermal conductance have lower limits: a certain level of metabolism is required to maintain basic functions, and the skin even with fully constricted vessels does not completely insulate the body. To maintain constant temperature, the production of heat must exactly compensate for the dissipation of heat. When possible, mammals keep their heat dissipation at minimum not to spend energy for regulatory thermogenesis.

Physical activity is actuated by muscle contractions, which are not extremely efficient processes. In fact, more than 80% of the energy generated in the muscles is wasted in the form of additional heat. This heat depends on the exercise intensity only. It may look like the best way to limit the temperature growth is to increase heat dissipation, which in both humans and rodents occurs in major part through an increase in blood flow in the skin. However, greater cutaneous blood flow competes with blood supply to other organs including muscles. That may be a reason why during exercise cutaneous vasodilation does not kick in until the temperature reaches really high levels[2] close to the fatigue threshold.

Heat dissipation can be represented as the product of the difference of temperatures inside and outside of the body and the thermal conductance of skin. In this context, one may think that at colder ambient conditions heat dissipation naturally increases due to a greater difference between the body temperature and the temperature of the environment. However, this higher dissipation occurs before the exercise even starts and, hence, is compensated by the thermoregulatory metabolic heat production.

Summarizing the above, cold environment cannot provide an ergogenic advantage through the lowering core body temperature unless metabolism unrelated to exercise is reduced. Thermoregulatory system may turn off or

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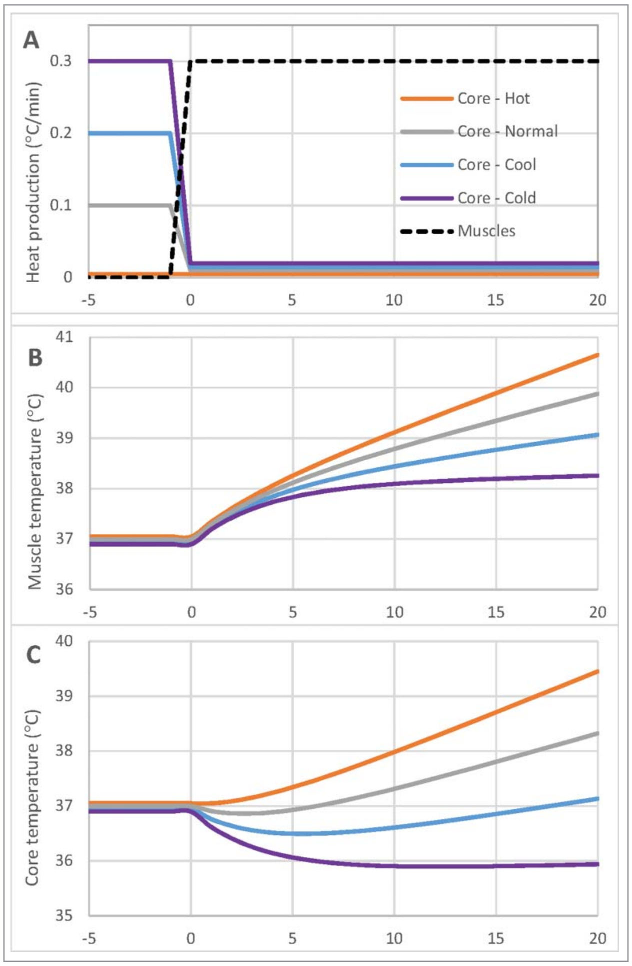

Figure 1. Model simulations of heat production (A), muscle temperature (B) and core body temperature (C) for progressively colder ambient temperatures (orange, gray, blue and magenta lines for hot, normal, cool and cold environment, respectively). Dashed line in A shows ambient temperature-independent heat production in the muscles. The run starts at t = 0.

suppress metabolic heat production when body temperature increases due to physical activity. To test this hypothesis we conducted a study[1] in which we measured body temperature dynamics in rats running on a treadmill with 4 different speeds and at 2 different ambient temperatures. The first thing we noticed was that before starting to rise, the body temperature dropped slightly during first several minutes of the run when the experiments were performed at normal room temperature ($T_a = 25°C$), and not at the higher ambient temperature we used ($T_a = 32°C$). In both cases there was a delay before the temperature began a steady growth. This effect was a strong indication that interactions between at least 2 compartments were involved in the observed temperature dynamics: in a single-compartment model, the temperature would start growing as soon as the heat production is increased. Another striking difference between the groups exposed to different ambient temperatures was that the rate of change of the core body temperature increased with the running speed for the hotter environment, but not for the normal room temperature.

To interpret this experimental data, we used a simple mathematical model which included 2 body compartments – the core and muscles - to calculate the changes in heat production in each compartment for all of the combinations of running speed and ambient temperature by fitting the model to our measurements. Additional heat generated in the muscles grew with the running speed in a manner independent of the ambient temperature. No significant changes in core heat production were observed at the high ambient temperature at any running speed. In contrast, at the normal room temperature there was a significant reduction in the core heat production. This reduction increased with the speed and saturated at 12 m/min at about 0.1°C/min. It is plausible that the saturation of the reduction in core heat generation reflects the level of the total thermoregulatory heat production for given ambient temperature. In other words, there was only 0.1°C/min available to reduce the metabolism. Similarly, no compensation was possible for $T_a = 32°C$ as the entire thermoregulatory component of metabolism vanished in the hot environment.

The two-compartment model explains the experimentally observed temperature dynamics very well and allows for meaningful predictions. Figure 1 illustrates the dynamics of heat generations and temperatures in the 2 compartments at the highest sustainable speed at various ambient temperatures with an assumption that initial temperatures in both compartments are the same.[1,3] In our experiments, rats were able to maintain the speed of 18 m/min with zero incline for more than an hour. Once the exercise begins, the heat production in the muscles increases to 0.3 °C/min (dashed line in panel A) and starts driving the muscle temperature up (panel B). In a hot environment the thermoregulatory component of the core heat production remains at zero before and during the exercise (orange line in panel A). The heat generated in the muscle with a certain inertia penetrates to the core causing a somewhat delayed growth of the core temperature (orange line in panel C). At normal room temperature the thermoregulatory metabolism is at 0.1 °C/min in the beginning but drops to zero as soon as exercise starts (gray line in panel A), resulting in slight hypothermia before the heat from muscle finally reaches the core and pushes the core temperature up (gray line in panel C). The model predicts, that the lower the ambient temperature is, the greater the reduction in the thermoregulatory metabolism may be (blue line in panel A), and the deeper and longer the hypothermic phase of the core temperature response becomes (blue line in panel C). When the drop in thermoregulatory heat production becomes comparable to the heat generation in the muscles (magenta line in panel A), the core temperature remains below the baseline for the entire run, which was, in fact, observed experimentally.[4]

In conclusion, we found that running causes the suppression of thermoregulatory thermogenesis which partly compensates for the increased overall heat production during exercise. Importantly, this suppression occurs as soon as the run starts, but before the body temperature is increased, and, thus, this phenomenon is not thermoregulatory in nature. Moreover, the initial core temperature response to exercise is hypothermic. Due to an increasing decline in core heat production, the rate of change of the core temperature progressively reduces with the ambient temperature, which increases the time until the core temperature reaches the thresholds for sweating and exhaustion.

An interesting implication of our study is that physical activity can be performed without any increase in metabolic load given that the initial thermoregulatory heat production is high enough. The phenomenon of "activity for free" was indeed previously described for species living in extremely cold environments.[5]

References

[1] Yoo Y, LaPradd M, Kline H, Zaretskaia MV, Behrouzvaziri A, Rusyniak DE, Molkov YI, Zaretsky DV. Exercise activates compensatory thermoregulatory reaction in rats: A modeling study. J Appl Physiol (1985) 2015; 119:1400-10:jap 00392 2015; PMID:26472864; http://dx.doi.org/10.1152/japplphysiol.00392.2015

[2] Tanaka H, Yanase M, Nakayama T. Body temperature regulation in rats during exercise of various intensities at different ambient temperatures. Jpn J Physiol 1988; 38:167-77; PMID:3172577; http://dx.doi.org/10.2170/jjphysiol.38.167

[3] Gavini CK, Mukherjee S, Shukla C, Britton SL, Koch LG, Shi H, Novak CM. Leanness and heightened nonresting energy expenditure: role of skeletal muscle activity thermogenesis. Am J Physiol Endocrinol Metab 2014; 306:E635-47; PMID:24398400; http://dx.doi.org/10.1152/ajpendo.00555.2013

[4] Guimaraes JB, Wanner SP, Machado SC, Lima MR, Cordeiro LM, Pires W, La Guardia RB, Silami-Garcia E, Rodrigues LO, Lima NR. Fatigue is mediated by cholinoceptors within the ventromedial hypothalamus independent of changes in core temperature. Scandinavian J Med Sci Sports 2013; 23:46-56; http://dx.doi.org/10.1111/j.1600-0838.2011.01350.x

[5] Humphries MM, Careau V. Heat for nothing or activity for free? Evidence and implications of activity-thermoregulatory heat substitution. Integrative Comparative Biol 2011; 51:419-31; http://dx.doi.org/10.1093/icb/icr059

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