PERSPECTIVES

Feeding the sleeping giant: muscle blood flow during whole body exercise

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One of the most startling physiological observations of the last 20 years has been the finding that blood flow to contracting skeletal muscle can be very high (Rowell, 2004). Before the 1980s it was widely believed that peak values for skeletal muscle blood flow during exercise were somewhere between 50 and 100 ml (100 g tissue)$^{-1}$ min^{-1} at 'reasonable' values of arterial pressure. Thus the ability for skeletal muscle to vasodilate was seen as limited.

However, in the 1980s observations using microsphere injections in animals suggested that blood flow to skeletal muscles performing heavy exercise could be substantially higher than previously believed. There were demonstrations in rats, dogs and horses of values on the order of 200–300 ml (100 g tissue)$^{-1}$ min^{-1}, and in some vascular beds (i.e. the diaphragm) even higher values were noted (Parks & Manohar, 1983; Armstrong, 1985; Manohar, 1986; Musch *et al.* 1987). The challenge of course was how to study this in humans.

This problem was especially difficult because the studies on animals had relied on the 'microsphere technique', an approach that is not suitable for human studies. Additionally, the observations in species such as dogs, while interesting, might not apply to humans since dogs are an 'athletic species' with very large heart-to-body weight ratios, high relative values of peak cardiac output and generally prodigious abilities to both transport and use oxygen. How then to solve this problem?

For determination of maximum skeletal muscle blood flow in humans to be possible several conditions had to be met. First, an isolated vascular bed with anatomically suitable blood vessels had to be identified. Second, a technique to perform isolated exercise had to be developed. Third, improved techniques to measure skeletal muscle blood flow were required. All of these challenges were met in the classic paper by Andersen (1985) where very high values of skeletal muscle blood flow were observed in humans during isolated quadriceps exercise. However, by solving the problem of just how high skeletal muscle blood flow might go in humans, Andersen and Saltin had awakened what Professor Loring Rowell (2004) has aptly called a 'sleeping giant'. Skeletal muscle is a sleeping giant because its capacity for vasodilatation could theoretically overwhelm the modest pumping capacity of the human heart and if this occurred arterial pressure, the main regulated variable in the cardiovascular system, might be threatened (Marshall *et al.* 1961). The question next became how to deal with this sleeping giant and how to manage the 'tug of war' between skeletal muscle vasodilatation, cardiac output, and the need for arterial pressure regulation. For a variety of technical and conceptual issues this seemingly simple question has been difficult to answer.

In this issue of *The Journal of Physiology*, Calbet and a team of Scandinavian colleagues under the leadership of Bengt Saltin (Calbet *et al.* 2004) report arm and leg blood flow values in highly trained, international-class cross-country skiers during maximal or nearly maximal leg and arm exercise performed alone and in various combinations. Using this approach conclusive evidence is presented that metabolic vasodilatation is restrained (probably by the sympathetic nerves) in the active muscle during heavy whole body exercise in humans. These observations in athletic 'experiments in nature' are especially helpful because all of the skiers' skeletal muscles are well trained, and all have an extremely high capacity for dilatation. These athletes also have very high maximum cardiac outputs, thus permitting the absolute maximum mass of active muscle to undergo peak vasodilatation before any fall in blood pressure might be seen. In this context, the authors estimate that mean arterial pressure during nearly maximum exercise with the arms and legs would fall to the mid 70s if the metabolic vasodilatation were not restrained.

This paper also represents an impressive chapter in the ongoing story of human physiology and highlights the major role that Scandinavian investigators and their key collaborators from all over the world play as our insight into the mechanisms and limits human adaptation continues to grow. Just as their forebearers used the harsh northern environment to probe the human condition in the ancient Sagas of Nordic literature, Scandinavian physiologists maintain an unwavering interest in using exercise and environmental stress to understand the limits of human physiological adaptation and regulation. Thus, the physiological story told by Calbet, Jensen-Urstad, van Hall, Holmberg, Rosdahl and Saltin demonstrates again that there are some questions that can only be asked and answered in studies conducted in alive awake human volunteers operating at or near the limits of their individual capacity. Hopefully, the approach taken by Professor Saltin's team also tells us something equally compelling about the maximum capacity of our species for curiosity, creativity, risk taking, perseverance and cooperation.

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