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EDITORIAL

A century of exercise physiology: key concepts in …

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The Editorial Board of the European Journal of Applied Physiology has endorsed a topical series in the theme "A Century of Exercise Physiology". History tells us that the importance of exercise in healthful living goes back to antiquity: Susruta (ca. 600 B.C.) in India, Hippocrates (460–370 B.C.) in Greece and Galen (129–210 A.D.) in Rome (Berryman 2010; Shephard 2013; Tipton 2014). The Eighteenth Century saw exercise being promoted as a medical intervention, as exemplified by the London physician Francis Fuller who in 1705 published "Medicina Gymnastica or A Treatise Concerning the Power of Exercise, with Respect to the Animal Oeconomy; and the Great Necessity of it in the Cure of Several Distempers"(Fuller 1705). However these recognitions of the importance and power of exercise do not mean that the physiological concepts underpinning present-day understanding of exercise were understood at that time, or even recognized. It was only during the past 300 years that important advances in understanding were made using the scientific methods of experimentation, observation, careful recording of data, logical interpretation and inference, and the publication of results. These practices facilitated, if not dictated, the development of new theories and concepts in exercise physiology.

The idea for this series comes from groupings of seminal research papers published in the first three decades of the Twentieth Century that established the foundations of modern exercise physiology. On reviewing a hundred or so of these papers, several notable features arise. First, exercise physiology was a hot research topic then, and it has continued to be. Second, many of the key journals publishing the work of these pioneering exercise physiologists have consistently published in this area for more than a century, such as: American Journal of Physiology, Journal of Biological Chemistry, Journal of Physiology, Plügers Archiv (later becoming European Journal of Physiology) and Skandinavisches Archiv für Physiologie (later becoming Acta Physiologica Scandinavica and then Acta Physiologica). The European Journal of Applied Physiology came into being on Feb. 1, 1928 as Arbeitsphysiologie, with the first volume comprising five papers focusing on exercise and occupational physiology.

Third, many of the experiments performed by these early researchers were creatively and rigorously designed and executed, with these designs laying a foundation for work that followed. Fourth, a number of conclusions of these studies have been supported over the passage of time. Noteworthy too, however, is that some of the unsupported conclusions are still accepted as 'true' by many in the exercise and sports physiology domain, of which perhaps one of the more striking examples is the assertion that "lactic acid causes fatigue" in human subjects performing exercise (Jervell 1928). And fifth, a number of conclusions of these studies have NOT been supported with the passage of time.

The choice of the initial three decades of the Twentieth Century as the period within which to anchor the 'key concepts in exercise physiology' series is not arbitrary. This is a period of time that allowed for the flourishing of many disciplines of science, human physiology included. And perhaps especially human physiology, given the demands of warfare and the necessary sequelae of medical treatment and therapies aimed at functional recovery, such as Pilates (summarized later by Pilates 1945). Influential publications accrued from key pioneers in the discipline of exercise physiology, with August Krogh and Archibald Vivian Hill each being awarded the Nobel Prize in Physiology or Medicine (in 1920 and 1922, respectively). One can point to:

1) John Scott Haldane and Claude Gordon Douglas (Oxford University) who had a productive collaboration in the early Twentieth Century that focused on ventilatory control and pulmonary gas exchange. For example, they concluded in 1909 that the hyperpnea during moderate exercise

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was mediated by a rise in PCO_2 in the respiratory centers (Haldane and Priestley 1905), also suggesting that it was slow in onset (Douglas and Haldane 1909). Douglas would later report a close association between ventilation and CO_2 output during exercise (Douglas 1927), which is now one of the accepted tenets of exercise physiology.

2) Almost contemporaneously, August Krogh and Johannes Lindhard (University of Copenhagen) would present results at odds with those of the Oxford investigators, documenting an immediate hyperpnea at exercise onset which they ascribed to cortical irradiation, a precursor of what is now known as central command (Krogh and Lindhard 1913a). They were also at odds with regard to whether the physiological dead space increased during exercise (Douglas and Haldane 1912) or remained unchanged (Krogh and Lindhard 1913b); it is now widely recognized to increase, but less so than tidal volume such that the dead space to tidal volume ratio decreases. But it is Krogh's work on the role of muscle capillary recruitment during exercise in supporting tissue oxygen delivery that is most noteworthy and for which he was awarded his Nobel Prize (Krogh 1919a, b, c).

3) In 1923, David Barr and Harold Himwich (Cornell University) provided the first comprehensive description of arterial and venous blood acid–base status during moderate and high-intensity exercise in the Journal of Biological Chemistry "Studies in the physiology of muscular exercise" series (Barr et al. 1923; Barr and Himwich 1923a, b; Barr 1923; Himwich and Barr 1923). This was timely, given the limitations of using alveolar gas to infer arterial blood PCO_2 in the earlier Oxford and Copenhagen investigations.

4) It was also in the 1910s and 1920s that the analysis of heat production in isolated frog muscle by Archibald Vivian Hill (University College London) pioneered muscle metabolic mechanisms and muscle mechanics, thus opening the way to research investigating effects in different types of muscle fibers. Hill's work, together with the biochemical analyses of his Nobel co-Laureate Otto Meyerhof, led to the recognition of distinct aerobic and anaerobic metabolic mechanisms in exercising muscle (Hill and Meyerhof 1923). These principles were applied to exercising humans, leading to the concepts of a maximum O_2 uptake and an oxygen debt comprising a fast component reflecting intramuscular oxidative conversion of lactate to glycogen and a slower component reflecting delayed oxidation of lactate that had diffused out of the exercised muscle (Hill and Lupton 1923).

And 5) In 1927 Harvard University's Harvard Fatigue Laboratory was established with Lawrence J Henderson as its titular Head but under the scientific leadership of D. Bruce Dill. Over the next two decades, the Laboratory would prove to an influential international force in many areas of exercise physiology (Tipton and Folk 2014). Dill's work over five decades set a standard for integrative investigation that began with the impressive series "Studies in muscular activity" (Bock et al. 1928a, b, c, 1932; Talbott et al. 1928; Dill and Fölling 1928; Dill et al. 1930) covering areas such as cardiorespiratory physiology, pulmonary gas exchange and metabolism. Of particular significance at the start of the 1930s was the revisionist evaluation of the Hill-Meyerhof concept by Margaria, Edwards and Dill (Margaria et al. 1933): the fast (alactic) component being ascribed to phosphocreatine resynthesis and therefore independent of lactate oxidation.

There are numerous other contributions dating from this period, deserving of mention being those of Francis Benedict and Edward Cathcart (Benedict and Cathcart 1913), Francis Bainbridge (Bainbridge 1919), Joseph Barcroft (Barcroft 1934) and Yandell Henderson (Henderson 1923).

The collective body of work of these investigators fueled the legitimizing of exercise physiology, both basic and applied, as an important area of research and study in its own right. But it would not be until the 1960s—nearly 40 years after the founding of the Harvard Fatigue Laboratory—that the first academic departments of exercise physiology would come into existence, exercise physiology previously having been largely subsumed within physical education departments. As a result, we are now in an era where the importance of exercise physiology in athletic achievement, physical and mental training, wellness and healthy living, injury recovery and post-trauma recovery therapies is to all intents universally recognized. Regular exercise is foundational to human health, both mental and physical (Booth et al. 2000).

In the present Century of Exercise Physiology Series the authors have set out to re-examine foundational research papers published between 1909 and 1930 and take the reader on a tour through the historical development of mechanisms contributing to our current understanding of exercise physiology. Each review highlights conclusions that have been supported *and* those that have not been supported over the passage of time. The key research driving increased understanding of function is highlighted, decade by decade, to build the story of our current understanding. And yes, there remain critical knowledge gaps and areas of controversy that underpin research efforts in hundreds of exercise physiology labs around the world. The papers in the series are *not* a historical step-by-step review of the literature. The focus is on the key concepts, and how these are linked together to bring us to our current state-of-the-science. The focus is on physiological mechanisms, not history.

In this issue of the Journal we present the first paper in the Century of Exercise Physiology Series. David Poole has taken on the task of developing our understanding of muscle oxygenation (Poole et al. 2021). The following issues will contain one or two reviews written by senior researchers whose work has spanned a significant portion of the past century. These are people who, through their published work, have embraced the historical foundations of their research area to guide their research progress.

As the series unfolds you may find that there are gaps. We therefore also invite you, the reader, to consider contributing to this series.

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