Biochimie 107 (2014) 161–166

Contents lists available at ScienceDirect

Biochimie

journal homepage: www.elsevier.com/locate/biochi

Review

Victor Henri: 111 years of his equation

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ARTICLE INFO

Article history:
Received 2 July 2014
Accepted 12 September 2014
Available online 20 September 2014

Keywords:
Victor Henri
Enzyme kinetics
Invertase
Experimental psychology
Spectroscopy

ABSTRACT

Victor Henri's great contribution to the understanding of enzyme kinetics and mechanism is not always given the credit that it deserves. In addition, his earlier work in experimental psychology is totally unknown to biochemists, and his later work in spectroscopy and photobiology almost equally so. Applying great rigour to his analysis he succeeded in obtaining a model of enzyme action that explained all of the observations available to him, and he showed why the considerable amount of work done in the preceding decade had not led to understanding. His view was that only physical chemistry could explain the behaviour of enzymes, and that models should be judged in accordance with their capacity not only to explain previously known facts but also to predict new observations against which they could be tested. The kinetic equation usually attributed to Michaelis and Menten was in reality due to him. His thesis of 1903 is now available in English.

1. Introduction

A recent paper [1] in the context of the centenary of Leonor Michaelis and Maud Leonora Menten's paper [2] discussed the work of their predecessor, Victor Henri [3,4]. They themselves were quite clear about their debt to him, but later authors have tended to be less so. In fact, the thesis that Henri wrote for his doctorate at the Sorbonne [4] contains ideas that still repay careful reading today, and to facilitate this we have prepared an annotated translation into English that forms the Supplementary material for this paper. Here we shall discuss why Henri's work continues to be important for biochemistry, after first drawing attention to his groundbreaking work in the field of experimental psychology [5–7], which is almost completely unknown to biochemists, and also giving a brief account of his later work in physical chemistry.

2. Henri's life and scientific career

As this is dealt with in detail in the Supplementary material and elsewhere [1,8,9] we give only a brief summary here. Henri (Fig. 1) was born in Marseilles in 1872, but despite his French name, nationality and place of birth he was wholly Russian in origin. His natural and adoptive mothers were sisters, and came from the very distinguished Lyapunov family: they were cousins of the mathematician Alexander Lyapunov, and Henri's niece married the physicist Peter Kapitsa. His early work was in experimental psychology, initially as assistant to Alfred Binet, the pioneer of intelligence testing. He spent a long period in Germany, and in one of his later visits he became acquainted with enzymes and physical chemistry in Wilhelm Ostwald's laboratory in Leipzig. Afterwards he moved from psychology to physiology, and from there to the mechanisms and kinetics of enzyme catalysis. In his later career he contributed to many fields, mostly with some relationship to physical chemistry, and at different times occupied major posts in France, Russia, Switzerland and Belgium. He died in La Rochelle in 1940. The principal steps in Henri's life and career are listed in Table 1.

3. Experimental psychology

Experimental psychology as a discipline came to prominence in the 1880s with the foundation of the first laboratories in Germany, the most famous being the one founded in Leipzig by Wilhelm Wundt in 1879. These laboratories were primarily intended to allow studies on the elementary forms (sensations, perceptions) of mental life. At the time, the French authorities wanted to develop experimental psychology, in order to follow the German research movement, and

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http://dx.doi.org/10.1016/j.biochi.2014.09.018

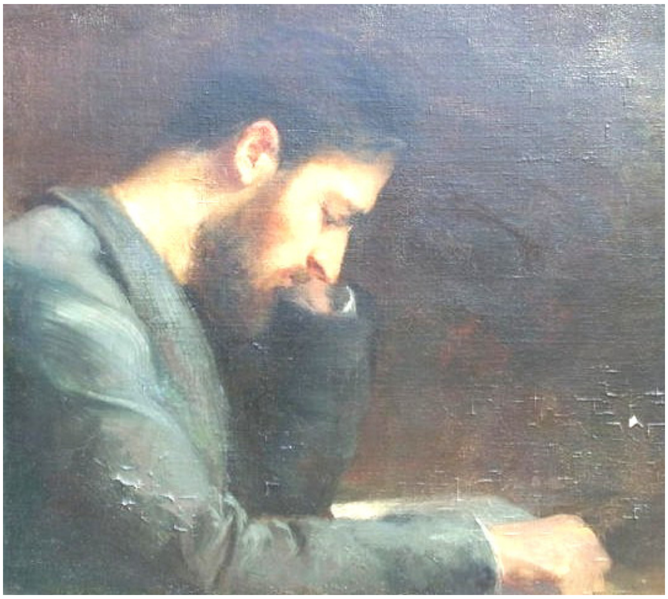

Fig. 1. Victor Henri. This is a detail from a painting by Mme. Laure Binet (wife of Alfred Binet), painted in about 1900. It is now in the possession of Mrs. Christine Henri, widow of Victor Henri's son Victor, and is published with her permission.

created a chair in the Collège de France in 1888 and a laboratory at the Sorbonne in 1889. As a young student of mathematics at the Sorbonne, Victor Henri was attracted by psychology as taught by Théodule Ribot at the Collège de France and by the new laboratory directed by the physiologist Henry Beaunis and his assistant Alfred Binet. When the first laboratory of experimental psychology was founded in Paris, work was first dedicated to the sensory domain. Henri was first interested by the study of the sensory domain working with hysterics at the Salpêtrière Hospital in the service of Jean-Martin Charcot under Binet's supervision. In 1892 Binet brought Henri into a research programme on memory, and he became a specialist in this new domain, writing papers in *L'Année Psychologique*, the journal of the laboratory, until 1901. The most famous one was a paper on infantile amnesia published in 1897 [10], now available in English [11], which inspired Sigmund Freud. It was impossible at that time to obtain a doctorate in psychology in France, and Henri decided to go to Germany. He studied with Wundt at Leipzig and Müller in Göttingen, obtaining a doctorate there in 1897 on tactile discrimination. During this period he kept French philosophical and psychological journals informed about the development of psychology in Germany [12,13]. He was an active researcher, and Binet enrolled him in his new programme of individual psychology.

Binet and Henri were dissatisfied with the studies made by their predecessors [14–17], which they considered incomplete, too much concerned with sensations that could easily be measured, and too little with higher intellectual processes. They undertook an extensive programme of research in which they set out to measure many aspects: memory; the nature of memory images; imagination; attention; the capacity to understand, observe, define and distinguish; suggestibility; aesthetic feeling; moral sentiments; muscular force and force of will; and motor ability. The ambitious nature of this programme is evident from the fact that even today some of these aspects, for example the nature of memory images, are not fully understood. Nonetheless, they devised a series of ingenious tests that could allow all of them to be assessed in about 90 min, and succeeded in making substantial progress. Their major paper from this work [5], now available in English [18], begins with a warning:

> We tackle here a new, hard and still very little investigated subject; you should not expect to find in our work final answers to the questions that will be raised. Our main purpose will be to indicate the problems with which individual psychology has to deal in order to highlight the practical importance it has for the teacher, the doctor, the anthropologist and even the judge…

Stimulated by this work with Binet, which also included studies of intellectual fatigue [6], Henri decided to study whether different degrees of intellectual effort had any physiological effect on the composition of the excretion products of subjects with a controlled diet and controlled muscular activity, which he called nutritional exchanges (*échanges nutritifs*) [7].

Binet continued with his psychological studies after Henri had moved on to physiology and physical chemistry, but we shall not discuss this here beyond mentioning his work on the measurement of mental capacity [19]. This has had enormous educational repercussions that continue to this day, though for many years it was applied in exactly the opposite way from what he intended: he believed that such tests could be used to identify children who needed specific kinds of remedial help, but in practice intelligence tests were long used for classifying children, and even adults, according to supposedly innate levels of ability [20].

4. Henri's research on enzymes

4.1. Introduction

After he left the psychology laboratory of the Sorbonne, Henri moved to the physiology laboratory, where he undertook very different research, becoming the pupil and close collaborator of Albert Dastre (Fig. 2), who supervised his work on enzymes. This is the main theme of this paper, and concerns the studies described by Henri in his thesis [4] (Fig. 3), principally of invertase, but also of elastase, emulsin and amylase. He approached all of these enzymes with a scientific rigour that can still stand as a model. In particular, he insisted that any explanation of a biochemical phenomenon must be consistent with the principles of physical chemistry, and that one should not use one explanation for some of the observed properties but a different one for others. This may seem to be too obvious to be worth saying, but papers continue to be published in which basic principles of thermodynamics and physical chemistry are violated, as well as models that are not internally consistent. In 1903 Eduard Buchner's overthrow of vitalism [21] was recent enough not to be universally accepted; it was still possible to believe that the laws of chemistry might not apply in full to biological systems, and thus Henri's attitude was advanced for its time. He was critical of his predecessors for failing to observe all of these principles, but he did not exempt himself, and was equally critical of a paper of his own [22] that he considered lacking in rigour: it proposed a model that was purely empirical but could not be applied over the whole range of substrate concentrations without invoking arbitrary changes in assumptions.

4.2. Invertase

Most of Henri's work dealt with invertase, which catalyses the hydrolysis of sucrose: sucrose + $H_2O \rightleftarrows$ fructose + glucose. The name *invert sugar* for the mixture of products, and the name *inversion* for the reaction, derived from the observation that the products rotate the plane of polarized light in a direction opposite from that of sucrose, and thus “invert” it. The name *invertase* refers, of course, to this. It was chosen for many of the early studies of enzyme action because, as an extracellular enzyme secreted into the medium by yeast, it is readily available for study, and because the reaction is easily followed polarimetrically.