

## CLASSICAL PERSPECTIVES

**Henry Head and his paradoxical reflex**

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In 1884 Henry Head was a 23-year-old medical student at Cambridge when he interrupted his medical studies to do research with Ewald Hering at the ‘German’ University in Prague. Hering had previously supervised a year’s work by Josef Breuer which led to the classic paper on the control of breathing through the vagus nerves (Breuer, 1868). This paper established the Breuer–Hering inflation and deflation reflexes but was full of unanswered questions. Head answered many of them. He took 3 years over the research, and then a further 2 years before publication (Head, 1889*a,b*). This slowness and care were typical of Head. When he wrote a paper he read and corrected it five times; than placed it on a shelf

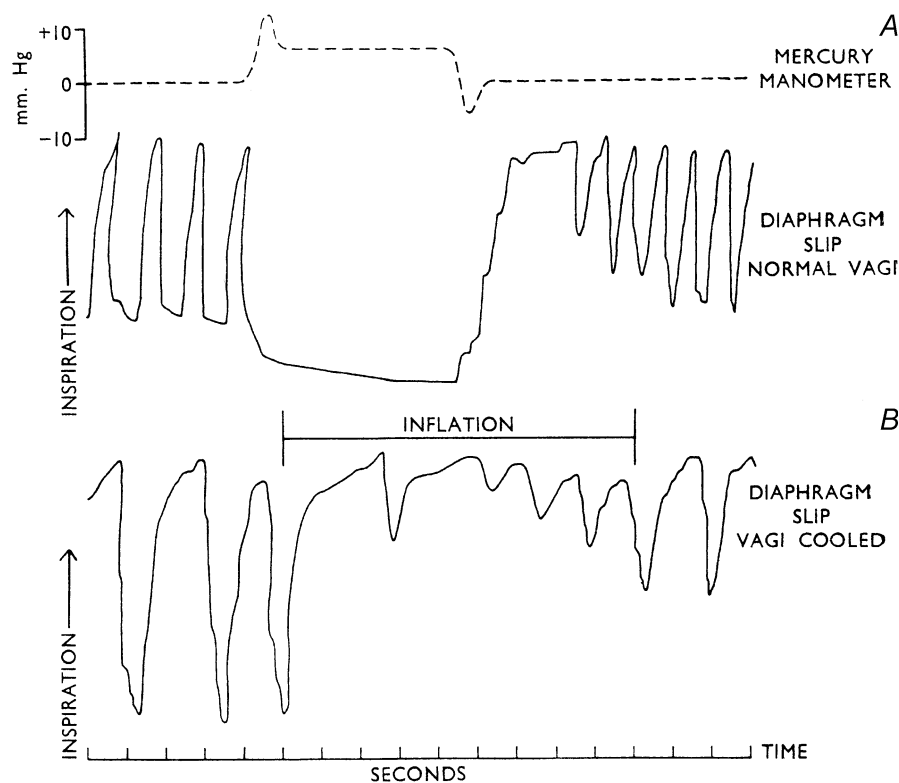
for a year before rereading it and submitting it for publication. Happy days!

Head split ‘On the Regulation of Respiration’ into two papers, ‘Experimental’ and ‘Theoretical’; they occupy 81 pages in Volume 10 of *The Journal of Physiology*. They are written with great clarity and precision and with meticulous attention to detail. They analyse the way in which lung volume changes in rabbits affect breathing via vagal reflexes. While no-one can doubt their nutrient value and digestibility they taste, nonetheless, like a large dollop of suet pudding. Yet buried in them are two sparkling little gems, well worth discovering.

Head took advantage of the method of Gad (1880) of reversibly blocking the vagus nerves by cold, so that controls could be done before and after blockade. And, more importantly, he established a method of recording diaphragm contraction from an isolated xiphisternal muscle slip (‘Head’s diaphragm slip preparation’). Previous methods allowed the stimulus of a lung volume change to interfere with what was

being measured—lung volume changes – unless one observed movements of the nares, a very indirect alternative. (Head was certainly an innovator. He made and used a cuffed endobronchial tube of rabbit size, 50 years before it was reintroduced by anaesthetists for humans. A ‘woodcut’ illustrates this in his ‘Experimental’ paper. Will *J Physiol* still accept woodcuts?)

The first of the two gems is a single page describing the discovery of the ‘paradoxical reflex’. When the vagus nerves were recovering from cold block, inflation of the lungs no longer inhibited inspiration (the Breuer–Hering inflation reflex, Fig. 1*A*), but strongly augmented it (Fig. 1*B*): ‘The strength of the inspiratory contractions is not increased but their duration is prolonged and... a tonic inspiratory contraction appears during the inflation’. Vagal section or further cooling abolished the response. He called the reflex ‘this paradoxical effect’ and said ‘I am totally at a loss to account for its appearance’. Earlier Breuer had said ‘It happened occasionally that, quite contrary to expectation, an animal responded



**Figure 1.** Redrawings from Head (1889*a*) made by Cross (1961)

The uppermost trace shows inflation pressure, the lower traces contractions of the diaphragm slip. *A*, the Breuer–Hering inflation reflex, showing relaxation of the diaphragm. *B*, Head’s paradoxical reflex, showing contraction of the slip, when the vagi were recovering from cold block. Reproduced from Cross KW, Head’s paradoxical reflex, *Brain* **84**, 529–534, by permission of Oxford University Press.

to distension of the lung by air inflation with an inspiration instead of an expiration'; and 'Obviously, in such animals only reactions that are entirely consistent merit attention'. Head found consistency and gave the reaction his attention. He had also discovered one of the few examples of positive feedbacks in the nervous system.

Fifty years later the sensory mechanism of the paradoxical reflex was analysed by Larrabee & Knowlton (1946). They showed that it was mediated by rapidly adapting pulmonary stretch receptors (RARs) in the lungs, with properties quite distinct from those of the slowly adapting receptors (SARs) responsible for the Breuer-Hering inflation reflex. Later it was shown to be important in the first breath of babies (Cross, 1961) and in causing augmented breaths that reverse the tendency of the lungs to collapse during quiet breathing (Davies & Roumy, 1982).

The second gem is the solution to a question left open by Breuer. He had shown that inflation of the lungs inhibits and deflation stimulates inspiration (the inflation and deflation Breuer-Hering reflexes), thus establishing the mechanism of the vagal reflex control of the pattern of breathing. But he didn't know if this was one or two reflexes. Since inflation could activate a reflex pathway and deflation could lessen the tonic activity of that pathway, only one afferent pathway was needed. Of the two hypotheses—one or two reflexes—Breuer concluded: 'In the present state of this investigation I dare not proffer a definite suggestion as to which of these hypotheses is the correct one. I hope

to come closer to a conclusion by further experimentation'. These further experiments were either not done or not reported. Breuer slid down a slippery slope to become the founder of psychoanalysis.

But Head answered the question. 'If both lungs are allowed to collapse suddenly by puncturing the thorax a much stronger inspiratory effort is produced than if both vagi were divided and yet... both operations equally remove the inhibitory stimuli normally passing up the vagi from the lungs'. 'I think it is difficult to explain these differences unless we assume that collapse of the lungs below the normal volume produced an actual inspiratory stimulus'. He tucked these comments away in his 'Theoretical' paper.

Identification of both the paradoxical and the deflation reflex were made possible by the use of the diaphragm slip preparation and vagal cooling. Again, it took 50 years before Larrabee & Knowlton (1946) and later workers analysed the mechanisms and significance of this separate deflation reflex. They showed that the same sensory receptors in the lungs, the RARs, mediated both reflexes. They were activated by both lung inflations and deflations, and reflexly caused inspiratory activity.

I have selected less than two pages of Head's 81 page-long papers as having much importance today. I suspect that, if Head were alive today, he would agree. After Prague he returned to complete his medical studies at University College London, and then moved to the London Hospital and the Institute of Neurology, Queen Square, to become the

most distinguished British neurologist of the 20th Century. His work with Hering may have been a hiccup in his career as a neurologist, but it was very important to him. It taught him scientific method and critique. He acknowledged the influence of Hering in the preface to his great book on aphasia by dedicating it to him. We should remember Head for his contributions to respiratory physiology even if he himself seemed rather unaware of their significance.

Breuer J (1868). *Sber Acad Wiss Wein* **58**, 909–937.

Cross KW (1961). *Brain* **84**, 529–534.

Davies A & Roumy M (1982). *J Physiol* **324**, 389–401.

Gad J (1880). *Arch Anat Physiol, Lpz Physiol Abt, suppl.*, 1–32.

Head H (1889a). *J Physiol* **10**, 1–70.

Head H (1889b). *J Physiol* **10**, 279–290.

Larrabee MG & Knowlton GC (1946). *Am J Physiol* **147**, 90–99.

### Original classic paper

The original classic papers reviewed in this article and published in *The Journal of Physiology* can be accessed online at:  
DOI: 10.1113/jphysiol.2004.065367  
<http://jp.physoc.org/cgi/content/full/jphysiol.2004.065367/DC1>

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<http://www.blackwellpublishing.com/products/journals/suppmat/tjp/tjp311/tjp311sm.htm>