through the rise of temperature, the intensities of all orders diminish, but those of higher order much more than those of lower. The effect was foreseen by the Dutch physicist Debije, and the amount of it was actually calculated by him on certain assumptions. I have found experimental results in general accord with his formula. In passing it may be mentioned that as the crystal expands with rise of temperature the spacing between the planes increases and the angles of reflection diminish, an effect readily observed in practise.

This part of the work gives information respecting the movements of the atoms from their places, the preceding respecting their average positions. It is sure, like the other, to be of much assistance in the enquiry as to atomic and molecular forces, and as to the degree to which thermal energy is locked up in the atomic motions.

This brief sketch of the progress of the new science in certain directions is all that is possible in the short time of a single lecture: but it may serve to give some idea of its fascination and possibilities.

WILLIAM H. BRAGG

WALTER HOLBROOK GASKELL (1847–1914)

DR. WALTER HOLBROOK GASKELL, university lecturer on physiology and prælector on natural science at the University of Cambridge since 1883, died suddenly, after a short illness, on September 7, 1914. He came of a well-known Unitarian family in the north of England, and was born at Naples, on November 1, 1847. After receiving his preliminary education, he entered Trinity College, Cambridge, in 1865, subsequently taking a medical degree at University College, London, in 1878. At Cambridge, Gaskell was one of the earliest to come under the influence of Michael Foster, then prælector on physiology, and, at his instance, entered Ludwig's laboratory at Leipzig in 1874. Prior to Foster's advent, Gaskell had specialized in mathematics, being one of the wranglers in the Mathematical Tripos in 1869. From the date of his first paper, an important research on the vaso-dilator fibers of striated muscle,[1] the rest of his life was devoted to those researches on the motor mechanism of the heart and the sympathetic system which have made his name so well known in physiology and clinical medicine.

English physiology in the first half of the nineteenth century was represented mainly by the work of Sir Charles Bell (spinal nerve roots), Marshall Hall (reflex action), William Sharpey (ciliary motion), Sir William Bowman (theory of urinary secretion), William Prout (HCl in the gastric juice) and Thomas Graham (osmosis, colloids). In 1867 Michael Foster was Sharpey's assistant at University College, and, in 1870, at Huxley's instance, became prælector at Cambridge, while Burdon Sanderson became Waynefleet professor of physiology at Oxford in 1882. From the teaching and inspiration of these two men came most of the brilliant names which have distinguished English physiology in the later period, with the exception of Starling, whose name is associated with Guy's Hospital. Schaefer was a Sharpey pupil, and was persuaded by Foster to devote his life to research. Leonard Hill and Gotch were Oxford men. From Cambridge came Langley, Henry Head, Sherrington, Roy, Adami, Gowland Hopkins and Gaskell.

When Gaskell began to work with Ludwig, every one believed in the so-called neurogenic theory of the heart's action, introduced by Borelli in 1680, viz., that the heart's movements, beat and tonus are due to nervous impulses. A little before Borelli, Harvey, in his demonstration of the circulation of the blood (1628), had advanced the idea that the heart is a muscular force pump, propelled by its own internal heat. This mystic dogma (the myogenic theory) was stated in more modern form by Haller in 1757, viz., that the heart's contraction is due to an inherent "irritability" of its muscle, the stimul s being the entrance and passage of venous bl od through it. Both theories, neurogenic and myogenic, have had their ups and their dow s to date. The neurogenic theory was res ted by Legallois in

[1] *Proc. Roy. Soc. Lond.* 1877, XXV., 439–445.

1812, and seemingly confirmed by the Webers' discovery that stimulation of the vagus nerve will stop the heart (1845); and by the discovery of intrinsic nerve ganglia in the heart by Remak (1848) and Bidder (1852), which were thought to be involved in the celebrated experiment of Stannius (1852), viz., that a ligature or cut between the sinus venosus and the auricles produces standstill, while a second ligature applied to the auriculo-ventricular groove causes the ventricle to beat again. The modern revival of the myogenic theory is the work of Engelmann and Gaskell.

Between 1874 and 1881, Gaskell made a long series of ingenious investigations upon the musculature and innervation of the heart, the results of which, as given in his great memoir of 1881[2] and later, may be summarized, however inadequately, as follows:

1. The motor impulses from the nerve ganglia in the sinus venosus are discrete, not continuous, stimuli, influencing the rhythm of the heart (its rate and force) but not originating either its movements or its beat.

2. Cardiac muscle can contract of itself and is a stimulus-producer. The five properties of cardiac (or other) muscle, as deduced by Gaskell, are excitability, conductivity, tonicity, rhythmicity and automatic contractile power. This power of automatic, rhythmic contractility has been recently confirmed in Burrows's extra-vital cultures of embryonic heart muscle,[3] which contain no nervous tissue whatever.

3. That the automatic contraction wave proceeds from sinus venosus to ventricle without nervous intervention is proved by Gaskell's and Engelmann's sections in the cardiac muscle, excluding the nervous tissues, and leaving only a narrow isthmus for the transmission of the rhythmic impulse. Gaskell reversed this peristaltic wave by stimulating the ventricle after the second Stannius ligature, showing that the normal impulse could not have started from the cardiac ganglia.

4. Gaskell first produced experimental "heart-block" (a term of his invention) by clamping the auriculo-ventricular and sino-auricular grooves, which he calls "the two natural blocking points" of the muscular contraction wave. In his view, the original Stannius experiments become simple cases of temporary block. This view has been brilliantly confirmed by the discovery of the vestigial muscular structures known as the auriculo-ventricular bundle of His and the sino-auricular node of Keith and Flack; also by the clinical and pathological findings in the disease described by Morgagni in 1761 and now known as heart-block or the Stokes-Adams syndrome. Gaskell even produced the two-, three- and four-time gallops of modern clinicians, in which the ventricle drops one or more of its beats. Schiff's observation that the ventricle of a dying heart beats slower than the auricle is interpreted as the effect of a gradually increasing block. Gaskell also produced the clinical condition known as "fibrillation of the heart" in an isolated strip of cardiac muscle, interpreting the phenomenon as due to blocking of the connections between individual muscle cells. In recent medicine, the various rhythmic disorders of the heart are regarded, not as cases of nervous imbalance, but as the effects of blocking of the peristaltic wave which passes from sinus venosus to bulbus arteriosus, and from muscle fiber to muscle fiber.

5. Schmiedeberg's observation that stimulation of the vagus after administration of nicotine will accelerate the heart led Gaskell to a series of investigations in comparative histology. He found that the hearts of warm-blooded and cold-blooded animals have the same innervation, that the inhibitory fibers of the vagus are medullated, the accelerator fibers non-medullated, leading to the important conclusion that both sets of fibers belong, not to the cerebro-spinal system, but to "the great system of efferent ganglionated nerves" (autonomic system), the function of which is the redistribution of impulses along collateral paths by means of fibers passing to and from an especial sympathetic ganglion or synapse. The efferent nerve cells of the inhibitory system lie in the heart itself, those of the accelerator system lie in external sympathetic ganglia, the nerve cells in either case being a switch (Foster's synapse) for the transmission of impulses. In 1890, Langley showed that nicotine will paralyze the medullated or pre-ganglionic fiber of a sympathetic ganglion without affecting the non-medullated (post-ganglionic) fiber. Schmiedeberg's experiment was, therefore, only a special case of Langley's nicotine effect. He was really stimulating the preganglionic or inhibitory fibers of the vagus; the switchboard effect across the synapse was abolished, the accelerator fibers from the external ganglia being unaffected by the poison.

[2] *Phil. Tr.*, Lond., 1883, CLXXIII., 993–1033.

[3] SCIENCE, 1912, XXXVI., 90–92.

6. The vagus, therefore, acts both as whip and bridle, spur and snaffle to the heart. The intrinsic ganglia being only bridges for the transmission of impulse, the true function of the vagus, in Gaskell's view, is not inhibitory but *quiescent*, acting upon the heart muscle itself. Gaskell revives Borelli's hypothesis[4] that the effect is chemical. The vagus is defined as the anabolic nerve of the heart. Inhibition is anabolism.[5] The vagus is a trophic nerve, both for muscle and ganglia.

7. Galvanometer observations showed that stimulation of the accelerator and inhibitor fibers produced opposite electrical effects which were independent of contraction, since they could be observed in a quiescent heart. These electromotive effects were first mapped and measured by A. D. Waller in 1889. Einthoven's string galvanometer made it possible for the physician to obtain "electrocardiograms" or telegrams from the heart, giving its electromotive condition, a field of investigation which Gaskell was the first to enter.

8. Gaskell regards certain discrepancies in the findings of experimentation upon the heart as due to chemical and nutritive changes in different hearts at different times of the year.

These results, the most important work on the heart since Ludwig, are embodied partly in Gaskell's Croonian Lecture of 1881, and, in more mature and complete form, in his splendid monograph in Schaefer's "Physiology" (1898). His comparative researches on the innervation of different animals lead him to his next great work, the mapping out and interpretation of the nerve supply of the entire vascular and visceral systems, culminating in his exhaustive memoir of 1886.[6] In this, it was shown, by microscopical observation, that the supply of nerves from the spinal cord to the chain of sympathetic ganglia originates mainly from the thoracic and upper lumbar regions, in which white rami, made up of medullated nerves, form the connection. Although it is now known that the cerebrospinal system alone governs reflex actions, it was formerly supposed that the sympathetic system was also concerned in the change of afferent impulses to efferent. The mapping out of the sympathetic nerves in their distribution from the spinal roots between the second thoracic and second lumbar vertebræ and the inclusion of the nerves proceeding from the cranial and sacral nerve roots, as a part of a greater system, distributed to the viscera, blood vessels, ductless glands and all organs or regions supplied by smooth (involuntary) muscle, was the special work done by Gaskell. This system was defined and interpreted by Langley as the "autonomic" system, the function of the sympathetic and cranio-sacral autonomics being the redistribution of impulses along all efferent paths which do not terminate in voluntary muscle, these paths proceeding from a neuron in the spinal cord to an external sympathetic ganglion or synapse, from whence the post-ganglionic fibers pass to the glands or muscles. The study of these paths began with Gaskell's investigations on the accelerator nerves of the heart. Langley's nicotine method proved the means of isolating individual synapses, as the drug acts selectively on the autonomic ganglia and not on the cerebro-spinal. In internal medicine, the connection of the autonomic systems with the ductless glands forms part of the interesting theory of the correlation of the internal secretions advanced by the Viennese clinicians, Eppinger, Falta and Rüdinger.

The remaining years of Gaskell's life were taken up with his theory, formulated in 1889, that the central canal of the nervous system was originally the lumen of a primitive gut, which is elucidated at length in his book on "The Origin of Vertebrates" (1908). In 1893, in connection with his work on the Hyderabad Chloroform Commission, Gaskell,

[4] Borelli believed that a contracting muscle actually increases in bulk through a fermentation started in its substance from a hypothetic "*succus*" discharged from the nerve.

[5] This view is opposed by Langley, and it does not harmonize with the experiments on isolated hearts in Ringer's solution by Howell and others. The limiting semi-permeable envelope of a living cell, organ or body is usually regarded as the agent of anabolism, preventing the undue dissipation of energy.

[6] "On the Structure, Distribution and Function of the Nerves which Innervate the Visceral and Vascular Systems," *Jour. Physiol.*, Lond., 1886, VII., 1–80.

with Dr. L. E. Shore, made an interesting contribution to pharmacology,[7] showing that chloroform lowers blood pressure by acting directly upon the heart, and not on the vasomotor center, as had hitherto been supposed.

Gaskell was an unassuming, sympathetic character, and it is said that every physiologist who has worked in the Cambridge Laboratory since its start was his personal friend. His eminent colleague, Professor J. N. Langley, thus describes him:

> Gaskell cared little for public ceremonies, and rarely attended the congresses which beset the path of prominent scientific men. He loved to work quietly, to cultivate his garden, to see his friends, and to take a hand at whist or bridge. His house at Great Shelford was a recognized meeting-place for physiologists, and his frank and genial welcome will be an abiding recollection to all who knew him.

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DR. GASKELL'S WORK ON ORGANIC EVOLUTION

IT is not with any idea of writing an appreciation either of the man or of his work as a whole that I venture to present this sketch. His work within the limits of the narrower field of physiology—the observations on the effect of a rise in tension of the muscles upon the caliber of the lymphatic vessels, the long series of experiments upon the relation of the vagus and accelerator nerves to the heart and on cardiac muscle, the work on the nerves to the salivary gland—has been dwelt upon by others.[1] I wish rather to call attention to some of the unusual features, and their bearing on the wider biological problems of the day.

Gaskell's work on the origin of vertebrates was begun under conditions that most investigators would consider unfavorable. His wife became afflicted with an obscure nervous disorder, not diagnosed at that rather early date, and his presence was required more and more at his home. Not wishing to give up investigation during his enforced absence from the laboratory, and having his attention turned toward the central nervous system, he began to enquire into its origin and development in the various animal phyla. Regarding the nervous system as the fixed and permanent structure in phylogenetic development, he concluded that the alimentary tract might be the thing to be made over in the transition from the invertebrate with ventral nerve cord to vertebrate with its dorsal nerve cord, and drew up his scheme of the origin of the vertebrates on this basis. Although Gaskell has brought together a vast amount of evidence bearing on this point,[2] his theory has been treated with scant courtesy by most morphologists. It is a common occurrence to hear it glibly and vigorously condemned by people who have never read his book or weighed independently for themselves the evidence adduced in support of the theory. It is worthy of remark in this connection that Gaskell was a pioneer worker in a line which has led in very recent years to the development of a large and important field in the morphology of the central nervous system—the field now included in the component theory of nerves. And he has shown in a way which has had its influence upon other theories of the origin of vertebrates, that the older idea of the formation of a new nervous system while the alimentary tract remained intact in phylogeny is not an assumption to be made lightly. But whether the theory of the origin of vertebrates as he propounded it be right or wrong, a matter which I venture to regard as still unsettled, certain of Gaskell's conceptions of the nature of fundamental biological processes are firmly and surely grounded. It is of these that I wish more particularly to speak.

Gaskell recognized very clearly the importance of the rôle played by internal processes in evolution. In 1910, he wrote:

> Now the formation of the Metazoa from the Protozoa and the progress of the Metazoa upwards signifies that the separate units composing

[7] Lancet, Lond., 1893, I., 386.

[1] Langley, *Nature*, 1914, Vol. 94, No. 2343, p. 93. *British Medical Journal*, 1914, No. 2804, p. 559.

[2] Gaskell, "The Origin of Vertebrates," New York and London, 1908.