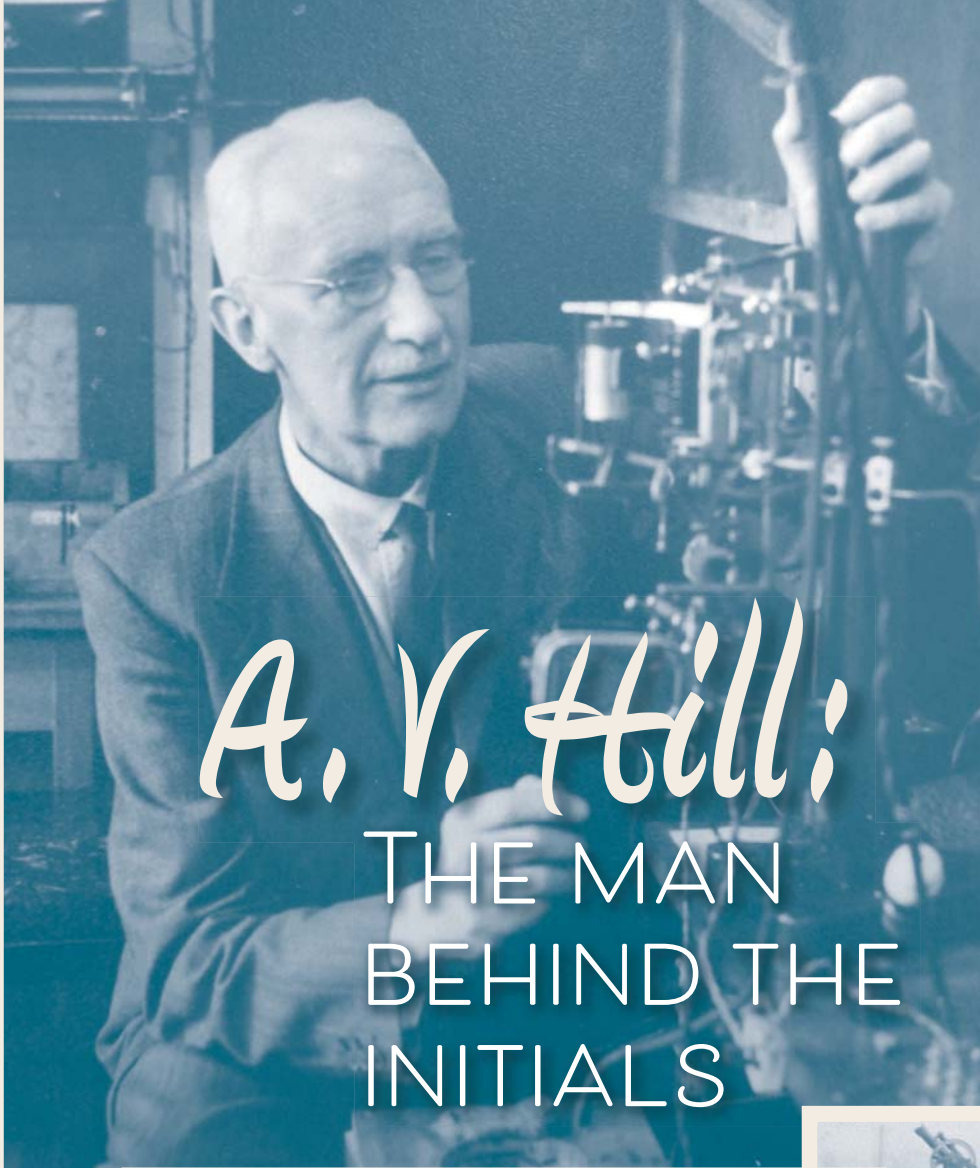
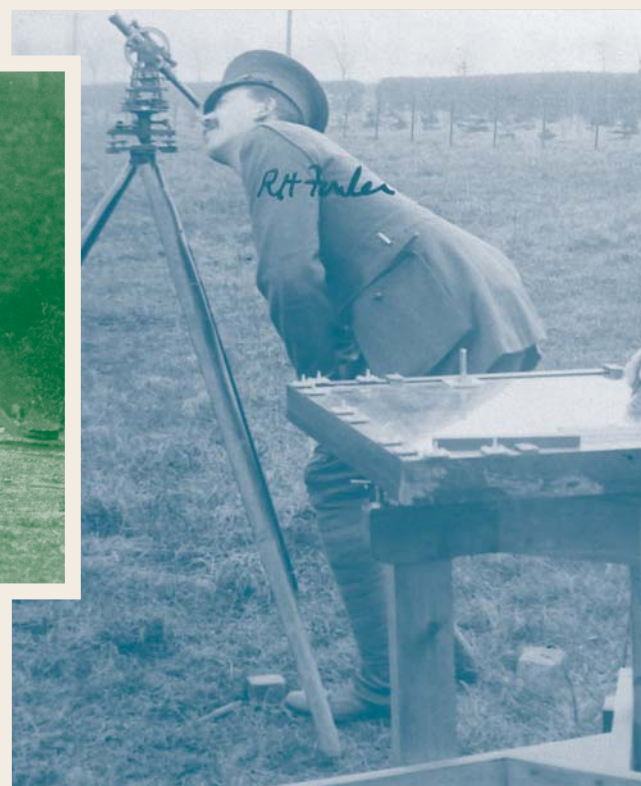
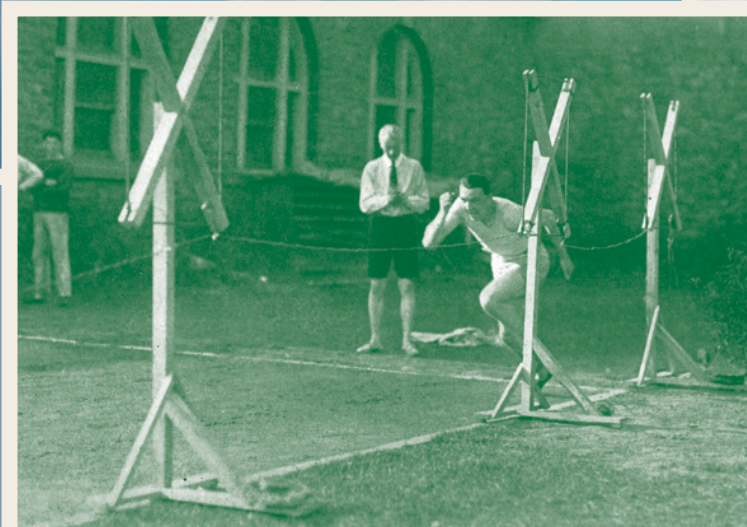




# A. V. Hill:

## THE MAN BEHIND THE INITIALS



Clockwise from top left: A. V. Hill in his laboratory in 1948; with a sprinter wearing a Douglas bag to measure his oxygen consumption; with the physicist Ralph Fowler (left), testing their prototype aircraft-position finder during World War I; and measuring a sprinter's acceleration at Cornell University in 1927. (The top two and bottom left images are courtesy of Nicholas Humphrey, and the bottom right image is courtesy of Nicholas Humphrey and the Churchill Archives Centre.)

**Andrew Brown** is a retired radiation oncologist. He has previously published biographies of James Chadwick, John Desmond Bernal, and Joseph Rotblat. *Bound by Muscle*, his book about A. V. Hill and Otto Meyerhof, will be published by Oxford University Press later this year.



## Andrew Brown

**The Nobel Prize winner was one of the founders of biophysics. He also helped rescue thousands of academics from Nazi-dominated Europe and contributed significantly to UK defense efforts in World War II.**



The morning he received word he would receive a share of the 1922 Nobel Prize for Physiology or Medicine, A. V. Hill rode to University College London (UCL) on his sidecar motorbike. Enthusiastic students carried him around the quadrangle before assailing Hill's distinguished predecessor as UCL's professor of physiology, Ernest Starling, in his laboratory. Because Hill's interests ranged far beyond the field's traditional boundaries, Starling had once joked that he did not know any physiology. The students taunted him with that remark, but Starling refused to give up the joke, exclaiming, "He doesn't know a damned word!"<sup>1</sup> All kidding aside, Starling held his successor in high esteem: When recruiting Hill to UCL, he accurately predicted that Hill would become the "most important person in the physiological world."<sup>2</sup>

Archibald Vivian Hill (1886–1977) was a physiologist, military scientist, and humanitarian. To most of his colleagues, family, and friends, he was known simply as "A. V." A central figure in UK science during the first half of the 20th century, Hill was also a prominent member of the international community. In the 1930s, he became an outspoken critic of fascism and was a cofounder, and subsequently the effective leader, of the Academic Assistance Council, which helped Jewish and anti-Nazi academics flee Germany and, later, Nazi-occupied Europe. In 1940 he laid the groundwork for the crucial Tizard Mission to the US and was elected as a member of Parliament (see figure 1). He extended his research beyond laboratory work on frog muscle to study the physiol-

ogy of exercise in humans and became a pioneer in the new subject of biophysics.

### Early life

After her marriage collapsed, Hill's mother, Ada, raised her two children alone. A. V. was competitive as a youngster and collected a series of scholarships that underpinned his education. The first was awarded to attend Blundell's School, a boarding school in Devon in southwestern England, where he excelled both academically and as a sportsman. Scholarships allowed him to attend Trinity College at Cambridge University, where he studied mathematics. He placed third in the famously grueling Wrangler exams in 1907.

Despite that success, the leading exam



coach of the era, R. A. Herman, cautioned Hill that he did not believe the student would make the grade as a mathematician. Although Hill never lacked self-confidence, he was realistic about his limitations and took Herman's opinion to heart. He discussed alternatives with his tutor, the physiologist Walter Fletcher, and decided to follow Fletcher into that field. Hill graduated with first-class honors in physiology in 1909 and, with fresh scholarship support, immediately embarked on a research career. In 1913 he married into the Cambridge academic aristocracy: Hill's bride, Margaret Keynes, was the daughter of the chief administrator of the university and the younger sister of the economist John Maynard Keynes.

### Physiology

In those days, physiology included the subjects that would now be termed embryology, histology, biochemistry, and pharmacology. The chief of the overcrowded physiology department was John Langley, who had succeeded the department's founder, Michael Foster. When Foster arrived at Cambridge from the Royal Institution in 1870, his working space consisted of one room with three tables. A purpose-built physiology laboratory would not be constructed until 1914. Despite the modest quarters, the group assembled by Foster and then Langley was highly talented. As Hill recalled, "There were probably more great physiologists there to the square yard than in any other place, before or since; and not only because there were so few square yards."<sup>3</sup>

Most of the physiologists at Cambridge, including Fletcher, were medical doctors, but Langley, like Hill, started his undergraduate life studying mathematics. A noted histologist, Langley conducted microscopic studies that distinguished sympathetic and parasympathetic nerves and clarified the structures of what he named the "autonomic nervous system." By the time Hill arrived in the department, Langley had turned his attention to the effect of such drugs as nicotine and curare on muscle stimulation. He had convinced himself that the drugs were effective because they combined directly with what he called "receptive substances" in muscle cells.

Langley wanted to find new evidence to support that theory, which his colleagues were skeptical of. One powerful approach would be to uncover the energetics of those reactions, and that was the task he set Hill. Perhaps Langley believed that Hill's mathematical prowess would allow him to succeed. In a remarkably short period—only a week or two—Hill immersed



**FIGURE 1. A. V. HILL** (right) on his first day as a member of the UK Parliament in 1940. (Courtesy of Nicholas Humphrey and the Churchill Archives Centre.)

specimens of frog abdominal muscle in solutions with varying concentrations of nicotine at different temperatures. Observing the time course of the contractions, Hill discovered that the muscle fibers relaxed completely when the nicotine solution was washed off. He found that both the contraction and relaxation phases could be accurately represented by two simple exponential functions.

Hill posed the question as to whether those curves could reflect a physical process in which the degree of contraction is due to nicotine passively diffusing into the muscle fibers, or whether his experimental results comported with Langley's hypothesis that the nicotine undergoes a chemical reaction

with a receptive substance. In his first paper, published in December 1909, Hill argued that his experiment was “very strong evidence in favour of the hypothesis of a [chemical] combination between nicotine and some constituent of the muscle.”<sup>4</sup>

He was always modest about that paper, but when his distinguished colleague and friend Bernard Katz read it closely while writing Hill’s obituary for the Royal Society’s *Biographical Memoirs*, he identified two important features buried in the main mathematical argument. As Katz pointed out, it was the first kinetic description of drug–receptor interaction, and it foreshadowed the 1913 discovery of the Michaelis–Menten equation, which deals with the reversible reactions of enzymes on substrates and is perhaps the most famous formula in all of biochemistry. Katz also showed that Hill anticipated Irving Langmuir’s 1918 paper on the adsorption of gases on metal surfaces. His reassessment of Hill’s first publication has gained general acceptance: It is regarded as foundational in both receptor theory and quantitative pharmacology.

## Hemoglobin

Two significant papers on hemoglobin followed within weeks. The first was an experimental study conducted with Joseph Barcroft, who had invented a manometer for measuring blood gases. He and Hill proved beyond doubt that the reversible union of oxygen with hemoglobin is a chemical reaction and that “the velocity of dissociation of oxy-haemoglobin obeys an equation derived from the laws of mass action, and has a high temperature coefficient.”<sup>5</sup>

The second paper, delivered at a meeting of the Physiological Society in London, analyzed the Bohr effect. That phenomenon was discovered in 1904 by the physiologist Christian Bohr (the father of Niels), who noticed the S-shaped curves that arise when the percentage saturation of hemoglobin with oxygen is plotted against the partial pressure of oxygen. Bohr observed that the oxygen-dissociation curves shift to the right as the concentration of carbon dioxide in the blood increases. Consequently, at higher levels of carbon dioxide, hemoglobin does not readily take up oxygen, which means that more is available to the tissues.

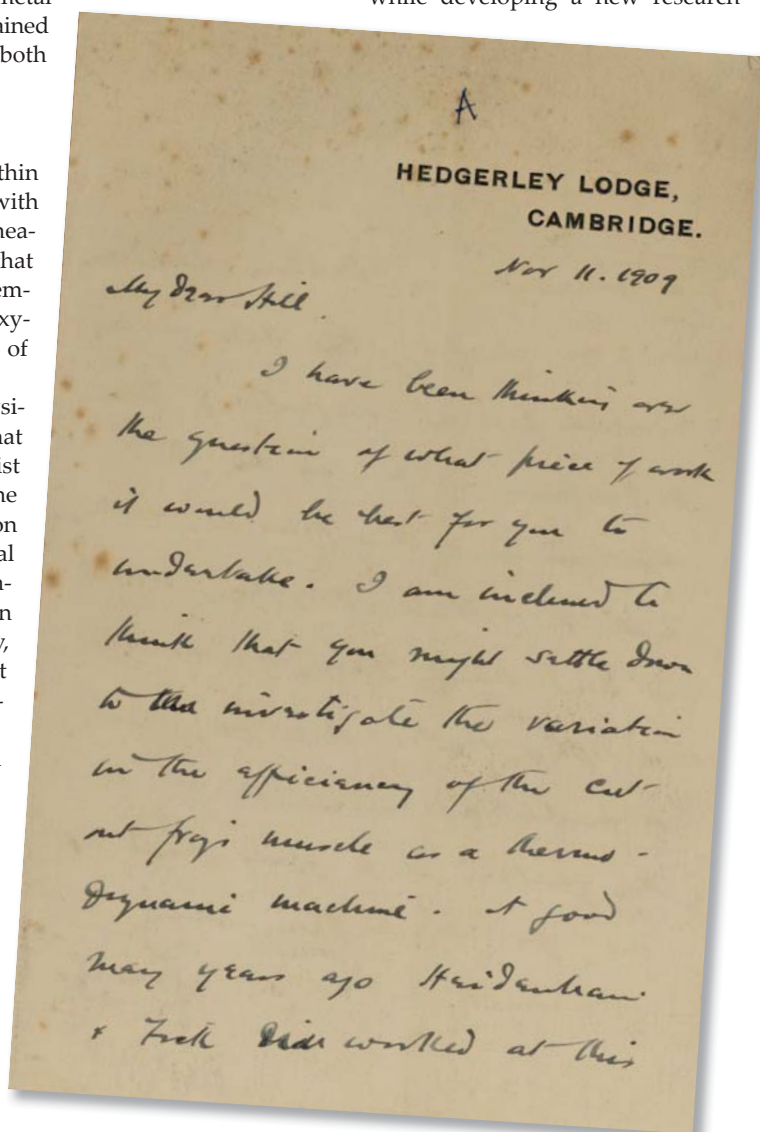
Hill’s paper derived a simple power equation, which he fitted successfully to published dissociation curves of hemoglobin in different chemical solutions. If the “Hill coefficient,” as it later became known, is greater than one, a positively cooperative reaction occurs, in which a macromolecule such as hemoglobin shows an increasing affinity for binding a ligand like oxygen after the initial link is made. The Hill equation has proven widely useful in pharmacology, physiology, and molecular biology.

Despite the brilliance of the two hemoglobin papers, Langley was particularly captivated by Hill’s first paper on frog-muscle contractions. Writing to Hill on 11 November 1909, Langley encouraged him to “settle down to investigate the variation in the efficiency of the cut-out frog’s muscle as a thermodynamic machine” (see figure 2). Hill considered that letter to be so important to his scientific development that, later in life, he glued it to the inside cover of a bound collection of his papers.

Hill’s chosen biological specimen, a thin slice of frog sartorius muscle, was dwarfed by his physical apparatus of galva-

nometers, thermocouples, novel electric circuits, and a rotating recording drum. He soon discovered that the frog muscle produced heat not only during stimulated contraction but also during the recovery phase. He realized that he was observing physical evidence of the underlying metabolic processes and concluded in a paper published in the *Journal of Physiology* in January 1911 that “the muscular machine is concerned with the transformations of chemical energy into the potential energy of increased tension.” That was the start of 50 years of studying similar phenomena. It would be the basis for his 1922 Nobel Prize.

Hill took the chair in physiology at the University of Manchester in 1920, where he continued his frog-muscle studies while developing a new research



**FIGURE 2. IN THIS LETTER**, dated 11 November 1909, the physiologist John Langley suggested to Hill that he “settle down to investigate the variation in the efficiency of the cut-out frog’s muscle as a thermodynamic machine.” (Courtesy of the Churchill Archives Centre.)



topic: the physiology of human exercise. Wearing Douglas bags on their backs that collected their expired air for analysis, Hill and his junior colleagues also measured their blood gases immediately after energetic runs. At sprinting speeds, they noticed that they incurred “oxygen debts” in their blood that rapidly increased and eventually prevented further effort. They were forced to repay the debt by consuming a huge volume of oxygen during subsequent rest. The term “oxygen debt” has since entered everyday speech, although other factors such as increased temperature and steroid levels are also involved.<sup>6</sup>

## Military defense expert

Hill was called up for army service at the start of World War I in 1914. His schoolboy talent for shooting meant he was soon training men bound for the trenches. In January 1916, he received an invitation from Horace Darwin—a son of the naturalist, Charles—to come to London to discuss a new project. Darwin oversaw the Anti-Aircraft Experimental Section of the Munitions Inventions Department, a UK governmental agency founded in 1915 to develop new military technologies.<sup>7</sup> He wanted Hill to study methods for accurately plotting the position of planes so that they could be shot down by artillery.

On the reluctant recommendation of Godfrey Harold Hardy, the mathematics don at Trinity College, Hill recruited the physicists Ralph Fowler and Edward Milne. The anti-aircraft group quickly expanded and moved to a naval base in Portsmouth, England, where they became known as Hill’s Brigands. Under Hill’s inspirational leadership, the brigands made numerous discoveries about the practicalities of antiaircraft fire and made the first rigorous mathematical analyses of artillery trajectories.<sup>8</sup>

As an imaginative experimenter who effectively directed a team and convincingly addressed problems in the field, Hill impressed senior military and government figures with his leadership qualities and his systematic approach. His brigands were among the first exponents of operational research. Fowler became the sole theoretician at the Cavendish Laboratory in the 1920s and would supervise dozens of doctoral students, including Paul Dirac. With Hill’s support, Milne became a leading astrophysicist and cosmologist during the interwar period.

Scientists at the Air Ministry remembered Hill’s wartime contributions in summer 1934 when they realized England’s vulnerability to attack from the skies. Although the national mood was lifting as the

country began to recover from the Great Depression, Winston Churchill rebuffed any such optimism in a fierce speech from the parliamentary back benches that warned about the threat from the expanding German Luftwaffe.

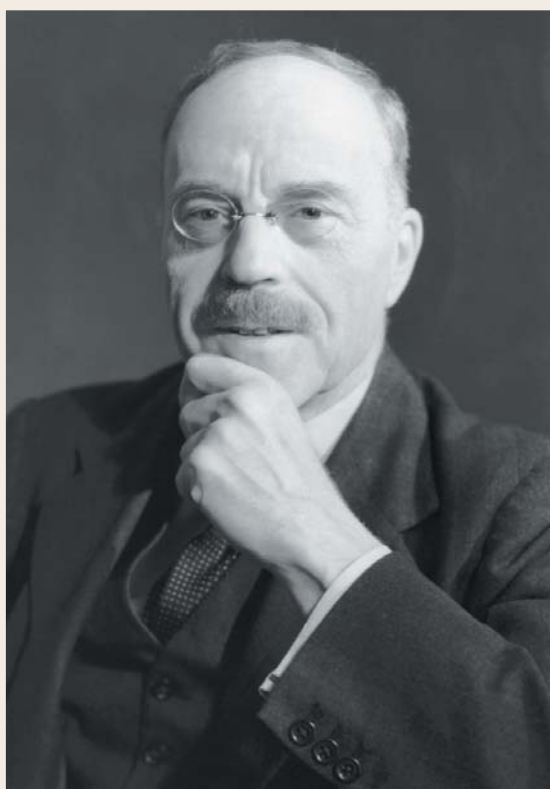
The message was reinforced by Churchill’s good friend, the Oxford physicist Frederick Lindemann, in an August 1934 letter to the *Times* of London. After a lunch with Hill at which the notion of using “death rays” against pilots was discussed, Harry Wimperis, the director of research at the Air Ministry, wrote to the secretary of state for air suggesting that a defense committee be established under the chairmanship of Henry Tizard (see figure 3). Tizard went to work immediately and included two independent scientists on his committee: Hill, whom he had known since 1916, and the physicist Patrick Blackett.<sup>9</sup> Churchill successfully pressed for Lindemann to be added to the committee (see figure 4).

Although Lindemann and Tizard had been friends since before the Great War, Lindemann’s addition to the Tizard committee destroyed its collegial spirit. He had a caustic personality and, worse, he disagreed with the committee’s emphasis on developing radar. Instead, as Hill later wrote in a 1960 letter to Lindemann’s biographer, the cantankerous physicist advocated a “fantastic scheme for dropping bombs, hanging by wires on parachutes in the path of attacking aircraft.” As a result Blackett and Hill resigned, but a new Tizard committee was soon formed, one which included them but not Lindemann.

## Anti-fascism

When he delivered the opening address to the International Physiological Congress in Rome in 1932, Hill shared the stage with Benito Mussolini and seemed to enjoy the encounter. Nevertheless, Adolf Hitler’s assumption of power in Germany in early 1933—which quickly led to unchecked anti-Semitism and the violent repression of all political opposition—filled Hill with foreboding. The Nazis quickly enacted a new law in April 1933 to “reform” the civil service. The law called for the dismissal of civil servants who had at least one Jewish grandparent or who opposed the Nazi regime. (An exception was initially made for Jews who fought for Germany in World War I.) Because all German universities were public institutions, the law had an immediate and deleterious effect on science.

Within one month, a relief organization to support German intellectuals began to take shape in the UK. The Academic Assistance Council (AAC), as it was termed, was largely the work of two men:



**FIGURE 3. HENRY TIZARD**, pictured here in 1942, led the UK air defense committee that championed the development of radar in the 1930s. (Photograph by Howard Coster, courtesy of the National Portrait Gallery, London.)



**FIGURE 4. FREDERICK LINDEMANN'S** caustic personality led to the temporary collapse of Henry Tizard's air defense committee. Lindemann (far left) is pictured here with Winston Churchill (with cigar) observing antiaircraft exercises. (Photograph by W. G. Horton, courtesy of the Imperial War Museums.)

the economist William Beveridge and the peripatetic physicist Leo Szilard. But Hill was soon drawn into the planning—he became a founding member and the organization's first vice president.

## HILL AND CRICK

Francis Crick started a PhD in physics at University College London in the late 1930s, but his studies were interrupted by the outbreak of World War II. After the war, as he wrote in a May 1947 letter to Hill, he began to feel "a strong, though uninformed inclination to some form of bio-physics." Hill invited Crick for an interview and told him he needed to learn some basic biology. Crick was not interested in muscle research, so Hill advised him to go to Cambridge, which he did in fall of 1947.

About 18 months later, Crick wrote to Hill that he had "looked more closely into x-ray analysis" and found it to be easier than he had anticipated. "I think I have the sort of brain which enjoys puz-

zles of this sort," he said. Crick applied successfully to join Max Perutz's Cavendish Laboratory group, which was studying protein structure. Crick's assertive personality and genius for x-ray crystallography was too much for William Lawrence Bragg, the Cavendish director. He wrote to his old friend Hill:

There is a young man working here, in Perutz's team, who I believe at one time was a protégé of yours and advised by you to take up biophysics. This is Crick. . . He is working for a Ph.D. here, though he is 35, because the war stopped him trying before. My worry is that it is almost impossible to get him to settle down to any steady job and I doubt whether

In November 1933, Hill gave the Huxley Memorial Lecture at the British Association for the Advancement of Science, in which he warned that the "coercion of scientific people to certain specified political opinions, as in Russia, Germany or Italy, may lower the standard of scientific honesty and bring science itself into contempt." A summary of the lecture was included in *Nature*,<sup>10</sup> which both inspired many repressed scientists in Europe and caused fury among Nazi party members.

Johannes Stark, the newly appointed head of the Imperial Institute of Physics and Technology in Berlin, took offense at Hill's accurate assertion that over a thousand scientists had been dismissed due to the Nazi law. In a brazen reply, which also appeared in *Nature*, Stark denied that anti-Semitism was a deliberate Nazi policy and that there were more than a few thousand people held in concentration camps. He accused Hill of

mixing science with politics. In a rebuttal, Hill dismissed Stark as an absurd anti-Semite and appealed for *Nature* readers to donate to the AAC.<sup>11</sup>

For many years, Hill was the essential executive at the AAC, which in 1936 was renamed the Society for the Protection of Science and Learning and is now known as the Council for At-Risk Academics. Much of the day-to-day responsibility for academic refugees and their families was unselfishly undertaken by the AAC's assistant secretary, Esther Simpson. She and Hill's largely unsung efforts led to salvation for more than

he has got enough material for his Ph.D. which should be taken this year. Yet he is determined to do nothing but research and is very keen to hang on here. With a wife and family he ought to be looking for a job. I think that he overrates his research ability, and that he ought not to count on getting a job with no other commitments. Are you interested in his career enough to wish to discuss it?<sup>18</sup>

Hill was interested enough to immediately reassure Bragg that Crick was worth keeping. Almost exactly one year later, Crick and James Watson announced the discovery of DNA's double-helix structure.

2000 scholars, including numerous future fellows of the Royal Society of London and Nobel laureates.<sup>12</sup>

## The Tizard Mission

In November 1935, Hill was appointed biological secretary of the Royal Society. By 1938, with war clouds on the horizon, Hill and other society officers began to compile a detailed registry of scientists and engineers whose services might be needed in wartime. Impressed by that effort, Tizard asked Hill in early 1940 to visit Washington, DC, as an ambassador for science. Hill readily agreed, and, upon his arrival that March, quickly established a good relationship with the UK ambassador.

Hill met with such leading scientists as Szilard and Enrico Fermi as well as the science administrator Vannevar Bush. He established contacts in Canada and attended the annual conference of the American Philosophical Society in Philadelphia. After that, he returned to DC for the annual meeting of the National Academy of Sciences. He made lists of US Army and Navy officers and organized names of engineers and physicists by the companies they worked for. He was impressed with the availability of young engineers in the US.

After one month in the US, Hill informed Tizard that the US military had paid little attention to radar, although strong commercial interest was developing. He argued that the US would quickly catch up and advised the UK government to “be frank, generous and immediate” in sharing the fruits of their radar research.<sup>13</sup> Although Tizard was convinced by Hill’s arguments, he faced considerable resistance in UK military and govern-

ment circles. But Churchill eventually agreed, and later that summer a black box of gadgets arrived in the US. Among the objects in the box was a prototype cavity magnetron, which enabled development of the centimeter-wavelength radar that proved vital to the Allied war effort.

The Tizard Mission, as it became known, was a triumph in establishing technical cooperation between the UK and US.<sup>14</sup> Although Hill did not take a direct role, it is hard to imagine that the mission would have happened without his ceaseless efforts during the first half of 1940.

## India

Just before going to North America, Hill took the oath of allegiance to the crown as a member of Parliament for the Cambridge University constituency. (Until university constituencies were abolished in 1950, several institutions of higher education were represented directly in the House of Commons; the voting body for each university constituency consisted of the respective university’s graduates. Isaac Newton, for example, was briefly a member of Parliament for Cambridge University.) Hill was elected as an Independent Conservative and, in a widely circulated memo, explained his reason for serving: “Practically none of the political leaders of the country have any personal acquaintance with science or technology.”<sup>15</sup> As he said, he aimed to make a nuisance of himself in Parliament, which he consistently did by deploring the treatment of refugees from enemy countries, attacking the government over its prosecution of the war, and, when he felt it was necessary, openly criticizing Churchill.

In early summer 1943, the Indian government invited Hill to visit, assess the state of scientific research, and advise how it might be harnessed for future development. Given the contentious state of politics on the subcontinent, Hill decided to undertake the task under the auspices of the Royal Society rather than as a member of Parliament. After several hops by flying boat, he arrived in Delhi and stayed in India for five months. His tour of universities, hospitals, schools, and factories was arduous, but his natural openness and friendly nature allowed him to quickly gain the confidence of new acquaintances (see figure 5). Hill gave lectures, compiled voluminous notes, and gave a broadcast on All India Radio.

In his report to the Indian government,<sup>16</sup> he recommended the establishment of an All-India Medical Centre and suggested creating a central department to oversee scientific research in the areas of medicine, industry, agriculture, natural resources, engineering, and war. Many of his ideas were adopted quickly, but Hill worried that India was living on the edge of a precipice because of disease, malnutrition, and population growth. He feared that internal strife or a disease outbreak like the 1918 influenza pandemic would produce a major catastrophe.

## Biophysics

On his return from India in 1944, Hill became engrossed in a Royal Society project on postwar needs. He was a strong proponent of biophysics and other interdisciplinary subjects. That December he circulated a memo arguing for the creation of a biophysics institute, in which he asserted that physical techniques such as radioactive labeling and electron microscopy should be adopted in the biological sciences.<sup>17</sup> The memo proved influential, and he succeeded in securing a substantial



**FIGURE 5. A. V. HILL** with the Indian chemist Shanti Bhatnagar. Hill’s 1945 report on the state of science in India helped determine science policy during the period leading up to Indian independence. (Courtesy of Nicholas Humphrey and the Churchill Archives Centre.)



grant in 1945–46 from the Rockefeller Foundation to start a biophysics department at UCL.

He persuaded Katz, a German Jewish refugee neurophysiologist who had studied with him in the 1930s, to accept the position of assistant director. Katz spent the war serving in the Royal Australian Air Force, in charge of a team running mobile radar units in New Guinea, where he gained much practical experience in electronics. The same was true for Hill's son David, his nephew Richard Keynes, and their Cambridge neurophysiologist friends Andrew Huxley and Alan Hodgkin. Hill regarded them all as physicists by nature who happened to have biological experience and knowledge.

Hill also placed journal advertisements that targeted young physicists coming out of the armed services who were thinking of switching to biology. Two notable recruits were Eric Denton, who later became the head of the Marine Biological Association's laboratory in Plymouth, England, and J. Murdoch Ritchie, who chaired Yale University's pharmacology department for many years. The one who got away was Francis Crick, who nevertheless owed his career start to Hill (see the box on page 43).

Although Hill continued to tinker in his UCL lab for years after World War II, he spent much of his time repeating previous experiments. His style as a physiologist was analogous to the empirical bent of Ernest Rutherford's school of physics, and he was slow to accept new theories such as the sliding-filament model of muscle contraction. Nevertheless, his popularity among his colleagues and the gratitude of those he helped to rescue from Nazi-occupied Europe brought him more accolades with each passing decade. Katz, one of those refugees, fittingly de-

scribed Hill in a 1996 autobiographical essay as the "most naturally upright man" he had ever encountered.

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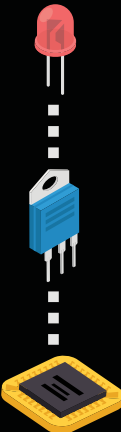
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