

THOMAS GRAHAM BROWN

1882-1965

Elected F.R.S. 1927

THOMAS GRAHAM BROWN was a neurophysiologist well known in the twenties for the detailed studies of reflex movement and posture which he made by Sherrington's methods, and perhaps better known in the thirties as the redoubtable climber who had found several new routes to the summit of Mont Blanc.

He was born in 1882 in Edinburgh. His father, Dr J. J. Graham Brown, was to be President of the Royal College of Physicians of Edinburgh in 1912 and was related to several of the eminent doctors who had maintained the reputation of the Edinburgh Medical School throughout the nineteenth century. It was natural therefore that the son should be trained to medicine and should go to his father's school, the Edinburgh Academy, and afterwards to the University as a medical student. There were four children in the family, Thomas, the eldest, a brother who became a Captain in the Royal Navy, one who became an architect and one sister. The two elder boys used sometimes to sail with their father in the yacht which he shared with a friend, and in Thomas the interest revived when he was too old for climbing but could still make long cruises in a small motor boat.

When he was a schoolboy he was fond of swimming and diving, skating and golf, but there was a period when his eyesight was troublesome and he was sent to an oculist friend of his father in Wiesbaden to be treated and to learn German.

As he grew up he showed a facility for pen-and-ink drawings with subjects ranging from the humorous to the architectural. He learnt to play a good hand at cards; he dressed carefully and was a welcome guest.

At the University of Edinburgh he was elected by his fellow students to be President of the Royal Medical Society and his academic work led to a B.Sc. 'Summa cum laude' in 1903 and to graduation with honours in Medicine in 1906. He was for a time Resident Physician at the Royal Infirmary and was then awarded the McCosh Medical and Travelling Scholarships of the University. He went to Strasbourg to work with Professor Ewald in his Physiological Laboratory and came back after a year with a sound knowledge of German and a definite intention to make his career as a physiologist.

Accordingly on his return in 1907, he became assistant to Professor Noel Paton in the Physiological Laboratory of the University of Glasgow and in



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1910 he was awarded a Carnegie Fellowship which took him to Liverpool to work in the laboratory of Professor Sherrington.

At that time Sherrington's reputation had already been established by his book *The integrative action of the nervous system*. His analysis of reflex activity had given a far clearer picture of the organization of the brain and spinal cord and there were still many details and some outlines to be filled in. Sherrington's laboratory was therefore the centre of attraction to all physiologists interested in the central nervous system.

Graham Brown had already developed this interest. When he was a medical student at Edinburgh he had worked for a time with Dr (afterwards Professor) Edwin Bramwell in the laboratory of the Royal College of Physicians. Bramwell's chief interest was in clinical neurology and he and Graham Brown started to investigate what was often regarded as a form of epilepsy which could be produced experimentally in the guinea-pig. It had been discovered in 1851 by the prolific neurologist, Brown-Séquard. He found that in the guinea-pig various lesions of the nervous system, and particularly section of one of the sciatic nerves, would often lead to convulsive attacks resembling those of epilepsy. They could be started by pinching the skin in a definite area, by electrical stimulation, etc., and they began with scratching movements of the hind limb leading to generalized convulsions.

For a time Brown-Séquard's 'experimental epilepsy' seemed likely to provide clues to epilepsy in man, but it had proved very difficult to decide the precise conditions which would lead to it: the percentage of guinea-pigs developing the attacks had varied from 100 in one laboratory to less than 10 in another and the percentage was considerably smaller in 1890 than it had been in 1875, though it appeared that the operative procedures were the same.

This variability, however, acted both as a hindrance to the investigator and a lure to make him persevere, for it raised the hope of finding some variable factor which might lead to epilepsy in man as well as in the guinea-pig. Graham Brown was a man of great determination and he did persevere for several years: in fact he published six substantial papers on the guinea-pig reactions, though they show a shift of interest, away from the causes of epilepsy and towards the general principles of nervous organization which were always the chief concern of Sherrington's laboratory.

Graham Brown held his Carnegie Fellowship at Liverpool from 1910 to 1913. He had freedom from teaching and administration, as well as the advantage of Sherrington's guidance, and his output in this period was greater than at any other time in his career as a physiologist. The work he did then is described in ten of the papers which he published in the *Quarterly Journal of Experimental Physiology* under the general title of 'Studies in the physiology of the nervous system'. These papers contain over 300 pages of experimental findings; the earlier refer to the reactions of the guinea-pig but in most of them the chief concern is with the factors which determine the reflex pattern from moment to moment.

In these researches Graham Brown was working alone, but there are also four which he published jointly with Sherrington. Two of these deal with the results of stimulating the motor cortex and particularly with the 'deviation of the response', the persistence of the same motor response when the stimulating electrode is shifted from one cortical point to another.

He returned to this problem in 1913 after he had left Sherrington's laboratory to become Lecturer in Experimental Physiology at the University of Manchester. Then came the war and in March 1915 he left Manchester for a war-time commission in the Royal Army Medical Corps, though he remained in England until the summer of 1916 and was able to write up some of his previous work. He was then posted overseas and served on various fronts, ending up in charge of the neurological work in the British Salonika Force.

In the Manchester period and until 1916 Graham Brown was still hard at work experimenting or writing up his previous work on the organization of reflex movements. By the end of that year the number of his 'Studies in the physiology of the nervous system' had risen from a total of 14 when he left Liverpool to no less than 27. No. 28 came out in 1924 and that was the last of the series.

By that time he had become Professor of Physiology at the Welsh National School of Medicine in Cardiff. He had ended the war run down in health and was not demobilized till November 1919. He returned then to his lectureship at Manchester but in 1920 he was appointed to the chair at Cardiff in succession to J. B. Haycraft. It involved the charge of a new institute with all its problems of staffing and equipment at a time when funds were scarce. In spite of these extra cares, he managed for some years to continue with his research, but after 1927 he published few papers, although from time to time he must have had the material for them, for he would enjoy demonstrating some new and interesting result. Meanwhile, although his department flourished, his interests were changing: he became gradually more and more concerned to find new routes in the Alps than to write more scientific papers.

Though he was a skilful and tireless experimenter with a sound knowledge of the anatomy as well as the physiology of the central nervous system, the outcome of his work was disappointing both to him and to those who realized its merit. It added to the general store of information on the spinal reflexes, yet apart from that it cannot be said to have had much influence on the progress of physiology. His purpose was to reveal the general principles governing the reflex response by comparing the details in each case, and his way of regarding reflexes as discreet entities seemed often to introduce an artificial element which affected the planning of the experiment. When Sherrington was at Oxford the main line of the advance had gone beyond the simple reflex; the chief interest lay in its cellular mechanisms, the stretch receptors and the motor units. Graham Brown, however, was still much more concerned with such questions as the form of the equation relating total

excitation to total inhibition. The final paper in the series of 'Studies in the physiology of the nervous system' is both a statement of the general object which he had in mind then and a proof that he realized the difficulty of reaching it.

Yet, although it may not have made a decisive advance, his work has the considerable virtue of independence. In several papers he introduced a conception of reflex activity which was not on the accepted pattern and is still useful. There are indications of it in his earlier work on the guinea-pig, but it is not fully elaborated until the papers published in 1914. The conception is that of a single reflex movement regarded as the product of a potentially rhythmic nervous apparatus like that involved in walking or running. In his earlier work he was at some pains to analyse what he called 'Narcosis progression'—the rhythmic kicking of the hind legs of a rabbit under ether—and he had found it occurring in deafferented limbs. This led to the conception of 'rhythmic half centres' in the spinal cord linked together and capable of beating rhythmically under balanced excitatory and inhibitory stimulation, though the rhythm could be altered by afferent impulses or by cerebral control and the same half-centre could produce isolated movement as well as the repeated discharge.

Graham Brown cherished his independence and led a rather lonely bachelor life at Cardiff, living at the Royal Hotel and spending most of his time in his workroom high up in the Physiology Institute or in his study on the first floor. He took great pains to see that the Institute was well equipped for teaching and research, but he found little time to establish personal contacts with his colleagues in other departments of the University or to encourage the casual foreign visitors who might be interested in his methods. To old friends he was a charming host and a welcome and undemanding guest but he had very few collaborators in his researches, perhaps because of his shyness or perhaps because he was unwilling to deviate from the programme he had planned for the investigation. On the other hand he used to speak very warmly of the help he had from the head of his workshop, A. L. Sims, who had been in H.M. Signal School at Portsmouth, and from his senior technician, T. J. Surman, who came from Sherrington's laboratory at Oxford. With their expert assistance he was able to begin some elaborate experiments on the walking and running movements of the decerebrate cat and on the wing movements of the pigeon.

As a professor in the University Graham Brown became known for the determination with which he challenged bureaucracy and supported the interests of his department. He was a formidable opponent and did not always conceal his pleasure in the fight and the victory. Yet his natural reserve was a barrier which was seldom broken down: and for some years there can have been few of his colleagues who guessed at the great ambition which had at first been no more than a dream but was now taking definite shape. It was the ambition to climb Mont Blanc by a new route up the Brenva face.

When this ambition was realized, his reserve evaporated. In the book which was published in 1944 under the title *Brenva* every chapter is headed by stanzas of poetry and he gives an intimate account of his hopes, adventures and triumphs. It begins with the story of his introduction to climbing in the Lake District. When he was with Ewald in Strasbourg and had been taken climbing in the Black Forest he had disliked the ubiquitous trees. The bare rocks in the Lakes made a much stronger appeal to him and his last holiday before the war was made memorable by a first ascent, up an unclimbed gully on Scafell. He had read A. E. W. Mason's story *Running water*, where there is an account of a climb on the 'old Brenva' route up Mont Blanc and this find on Scafell made him wonder whether there might not be new routes on the Brenva face where he could make another first ascent. During the war he found relief in day dreams of climbing there, and he describes (in poetry as well as in prose) a vivid recurrent night dream of a region of snow and mountains to be climbed by a variety of routes. The dream often began in Cumberland and included the Brenva face of Mont Blanc (which he had never seen).

Except in the dream he did not see it until 1926. The weather was bad, but a journey took him near enough to Mont Blanc to identify the 'Old Brenva' route and to think of a better. Next year he had the good fortune to meet F. S. Smythe at Montenvers. Smythe was already an experienced climber and like Graham Brown he had been with companions who had now left for home. They decided to climb together and, if possible, to find a new route on the Brenva face. Both had routes to suggest, but in the end, however, another was chosen. It was a long and arduous climb involving some risk from falling ice as well as a chilly bivouac, but all went well and the summit of Mont Blanc was reached on the afternoon of the second day's climbing. It is now called the Sentinelle Route and Graham Brown was naturally elated at having made such a first ascent.

It was not to be expected that his ambition would be fulfilled by this one success and he records that the reality did not quite come up to the dream. The climb, in fact, had gone too well, without unavoidable difficulties or severe physical and mental stress. He had spent a night of shivering in a bivouac-sack half buried in the snow and there was great deal of step cutting the next day, but these were the normal hardships of such a long climb in the Alps. He was well suited by temperament and physique to overcome them: his figure was compact and sturdy, on the small side but well proportioned, and he could pursue his aim with a relentless energy. It was no surprise that the Sentinelle route was only the first of many first ascents which he made in the Alps and afterwards in mountain regions in other parts of the world.

He and Smythe had considered two other routes up the Brenva face and in 1928 they made the first ascent of one of them, christened the Route Major. This was technically more difficult though less exposed than the Sentinelle route and poor weather added to the difficulties when they were

climbing it. After that it was five years before Graham Brown could attempt the third, the Via della Pera. He was no longer climbing with Smythe and had found a guide he could trust, Alexander Graven, who had the right enterprising attitude and was willing to share the leading and even relinquish it to his patron.

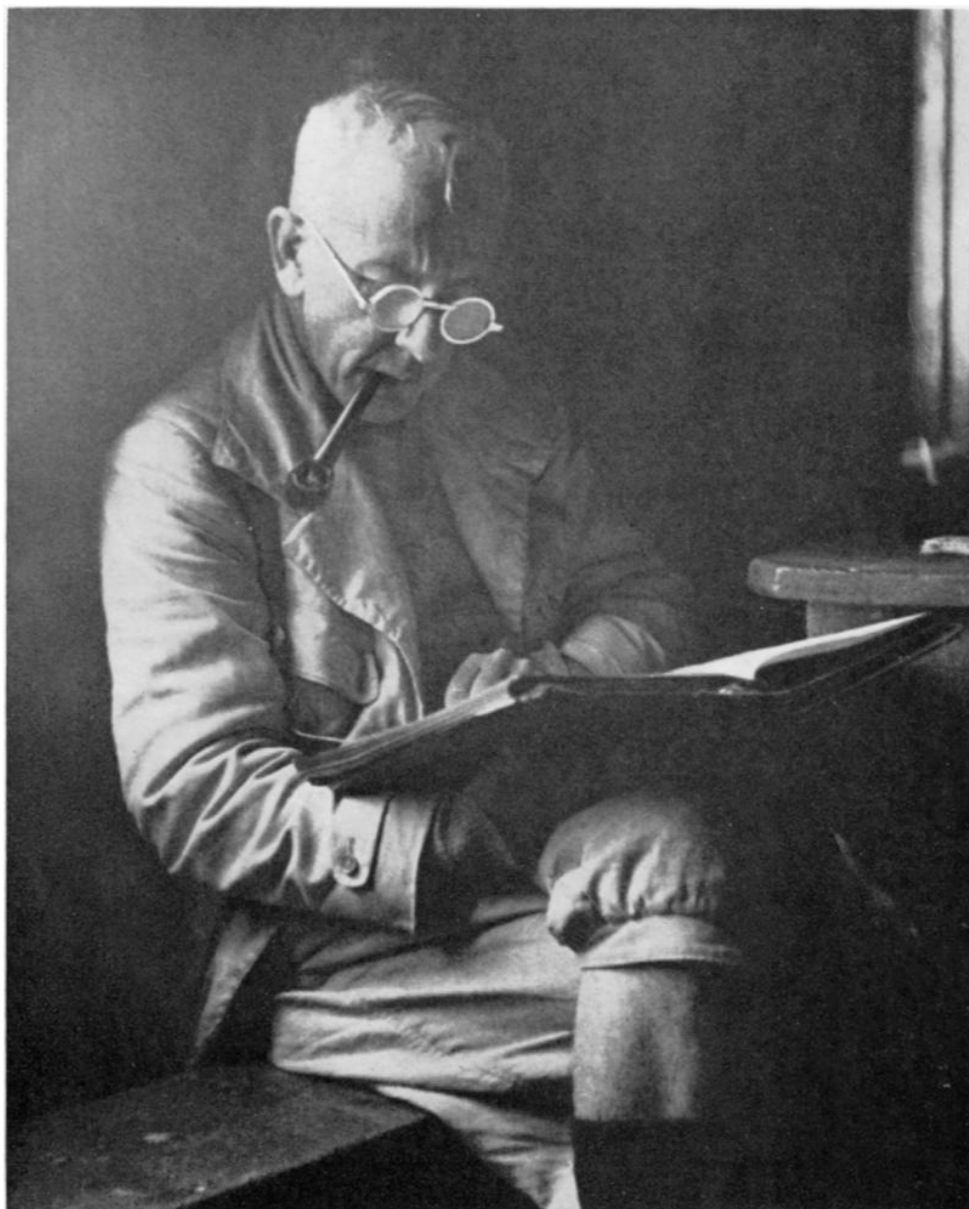
In the thirties Graham Brown was at the height of his powers as a climber. The planning of his holidays was not allowed to interfere too much with the needs of his department but there was no doubt where his chief interest lay. It took him much farther afield than the Alps, to Mount Foraker in Alaska, to Nanda-Devi in the Himalayas and later to Masharbrum in the Karakorams. He had become a well-known member of the Alpine Club, he wrote articles in *The Alpine Journal* and illustrated them with excellent photographs as he had illustrated his physiological papers with excellent kymograph tracings. His book on the Brenva climbs had been published in 1944, but he was editor of *The Alpine Journal* from 1949-1953 and in 1957, in collaboration with Sir Gavin de Beer, he wrote an authoritative volume on *The first ascent of Mont Blanc* to celebrate the centenary of the Alpine Club.

In 1947 he had reached the age of 65 and ceased to occupy the chair of physiology. His experiments had taken a new turn in 1935 when he began to use a moving platform to induce walking movements in the decerebrate cat, and a few years later he had studied the wing beat of the decerebrate pigeon moved through the air at different speeds. He had made some excellent films to illustrate these experiments and they were shown to the Physiological Society, but he could never be induced to publish an account of what he had found.

After he retired he abandoned experimental work and was mainly concerned with his mountaineering interests. He did not leave Cardiff, however, for he was invited to keep the room at the laboratory which held his books, papers and apparatus. This he regarded as a great privilege: he was often there all day, coming early before the main influx, and leaving after most of the staff had gone home, writing by the window with a pad on his knee and his pipe and matches on a stool beside him.

By that time the late effects of frost-bite contracted in the Karakorams had begun to trouble him and to curtail his outside activities. Yet he could still enjoy occasional climbing in Great Britain and helping to train teams in mountain rescue work, and he found another outlet for his powers of endurance. He acquired a motor boat converted from one of the smaller R.N.L.I. lifeboats, with a dinghy which had to be towed. In this he made long cruises around the British Coast and once with two companions as far as Tromsø in spite of heavy seas and the loss of the dinghy.

In 1961 when he was 79 he left Cardiff and his room in the Institute. There were inevitable reconstructions to be carried out in the laboratory and he would sooner or later have had to go to another room with all his belongings. Rather than face such a move he had decided earlier that he would return to Edinburgh and in 1958 he had bought a flat there close to



T. Graham Brown in the Promontoire Hut, 1933. (Photo by B. R. Goodfellow.)

the house where he had lived as a boy. At first he used it mainly as a base where he could keep some of his books and for a time to give house room to occasional students interested in climbing, but in his eightieth year his health began to fail and he was there as an invalid. He died on 28 October 1965 after a stroke, leaving a great deal of written material that he had never managed to put in order, records of experiments and of minor expeditions in the Alps or farther afield. The experiments might have ceased to interest him, but he had been more fortunate on the mountains. In his research on reflexes he had chosen what seemed to be a straightforward route. It would be classed as 'difficult'; surmounting the obstacles needed prolonged effort as well as a high level of technical skill. He had started well and had made his name as a scientist, but the route soon lost its direction. He must have realized that it gave little prospect of reaching the higher slopes and finding a way to the summit.

In the Alps he had done much better. The routes he had chosen would rank as 'severe'; they were long and exposed and he had reached the summit unscathed. But there was not much need to add to what he had written already. His great climbs are fully described in the book which was printed in 1944. That is his personal record and in it we learn about the author as much as he wished us to know.

For biographical details of Thomas Graham Brown I am indebted to his sister Mrs Jane P. H. Graham Brown of Edinburgh and to Professor J. M. Peterson of Cardiff.

ADRIAN

BIBLIOGRAPHY

Papers

1905. (With E. BRAMWELL.) Observations on Brown-Séquard's epilepsy. I. The incidence of Brown-Séquard's epilepsy in guinea-pigs as a sequel to section of the sciatic nerve. *Rev. Neurol. & Psychiatry*, **3**, 776-782.
1908. Der Einfluss des Nervensystems auf die Form der Zuckungskurve des Frosch-Gastrocnemius. Separat-Abdruck aus dem *Archiv. für die ges. Physiologie*. **125**.
1908. (With E. P. CATHCART.) On the creatin-creatinin content of frog's muscle. *J. Phys.* **37**, xiv.
1909. Studies in the reflexes of the guinea-pig. I. The scratch reflex in relation to Brown-Séquard's epilepsy. *Quart. J. Exp. Physiol.* **2**, 243.
1909. The 'Anaesthetic scratch' in guinea-pigs. *J. Physiol.* **38**, lxxxvii.
1909. A scratch reflex in guinea-pigs after removal of parts of the cerebral cortex. *J. Physiol.* **38**, lxxxvi.
1909. Die Atembewegungen des Frosches und ihre Beeinflussung durch die nervösen Zentren und durch das Labyrinth. Separat-Abdruck aus dem *Archiv für die ges. Physiol.* **130**.

1909. (With E. P. CATHCART.) The effect of work on the creatin content of muscle. *Biochem. J.* **4**, 420-426.
1909. Eine neue Methode, Herzbewegungen bei Tauben zu registrieren *Z. biol. Technik und Methodik*. Sonderabdruck aus Band 1, 282-284.
1910. Studies in the reflexes of the guinea-pig. II. Scratching movements which occur during ether anaesthesia. *Quart. J. Exp. Physiol.* **3**, 21-52.
1910. Studies in the reflexes of the guinea-pig. III. The effect of removal of the cortex of one cerebral hemisphere. *Quart. J. Exp. Physiol.* **3**, 139-170.
1910. Studies in the reflexes of the guinea-pig. IV. Some morphological changes associated with Brown-Séquard's 'epilepsy'. *Quart. J. Exp. Physiol.* **3**, 271-284.
1910. Studies in the reflexes of the guinea-pig. V. Some experiments on the influence exercised by the higher centres upon the scratch-reflex. *Quart. J. Exp. Physiol.* **3**, 319-353.
1910. Eine Methode, um Holothurien in ausgedehntem Zustande zu komserveiren: von A. S. Pearse (Ann Arbor, Mich., U.S.A.). Ein neuer Apparat zum Gebrauch bei der graphischen Aufzeichnung. *Z. biol. Tech. und Meth.* **2**, 94-96.
1910. Binaural localisation of sound. *J. Physiol.* **40**, 1.
1911. Studies in the reflexes of the guinea-pig. VI. On the relation between maintained contraction and rhythmic discontinuous inhibition. *Quart. J. Physiol. Exp.* **4**, 19-44.
1911. Studies in the physiology of the nervous system. VII. Movements under narcosis in the pigeon. Movements under narcosis in the rabbit—progression—scratching—flexion. *Quart. J. Exp. Physiol.* **4**, 151-182.
1911. Studies in the physiology of the nervous system. VIII. Neutral balance and reflex reversal, with a note on progression in the decerebrate guinea-pig. *Quart. J. Exp. Physiol.* **4**, 273-288.
1911. Studies in the physiology of the nervous system. IX. Reflex terminal phenomena—rebound—rhythmic rebound and movements of progression. *Quart. J. Exp. Physiol.* **4**, 331-397.
1911. (With C. S. SHERRINGTON.) Notes on the pilomotor system. *Quart. J. Exp. Physiol.* **4**, 193-205.
1911. The intrinsic factors in the act of progression in the mammal. *Proc. Roy. Soc. B*, **84**, 308-319.
1911. Note on the perception of movement of the environment. *Brit. Psychol. Soc.* June 24.
1911. (With C. S. SHERRINGTON.) Observations on the localization in the motor cortex of the baboon (*Papio anubis*). *J. Physiol.* **43**, 209.
1912. An alleged specific instance of the transmission of acquired characters. Investigation and criticism. *Proc. Roy. Soc. B*, **84**, 555-579.
1912. Studies in the physiology of the nervous system. X. A note upon 'Rebound relaxation after inhibition'. *Quart. J. Exp. Physiol.* **5**, 233-235.
1912. Studies in the physiology of the nervous system. XI. Immediate reflex phenomena in the simple reflex. *Quart. J. Exp. Physiol.* **5**, 237-307.
1912. (With C. S. SHERRINGTON.) On the instability of a cortical point. *Proc. Roy. Soc. B*, **85**, 250-277.
1912. The factors in rhythmic activity of the nervous system. *Proc. Roy. Soc. B*, **85**, 278-289.
1912. Notes on the final report of the Royal Commission on Vivisection. *Liverpool Medico-Chir. J.* July, 237-245.
1912. Note upon the movements of progression in man. *J. Physiol.* **45**, xvii.
1912. Note upon some dynamic principles involved in progression. *Brit. med. J.* September 28.
1912. (With C. S. SHERRINGTON.) The rule of reflex response in the limb reflexes of the mammal and its exceptions. *J. Physiol.* **44**, 125.
1913. Studies in the physiology of the nervous system. XII. Rhythmic responses in the simple reflex—progression—scratch. *Quart. J. Exp. Physiol.* **6**, 25-56.

1913. Studies in the physiology of the nervous system. XIII. The compounding of stimuli in temporal succession. *Quart. J. Exp. Physiol.* **6**, 209-249.
1913. The phenomenon of 'narcosis progression' in mammals. *Proc. Roy. Soc. B*, **86**, 140-164.
1913. On postural and non-postural activities of the mid-brain. *Proc. Roy. Soc. B*, **87**, 145-163.
1913. On the question of fractional activity ('all or none' phenomenon) in mammalian reflex phenomena. *Proc. Roy. Soc. B*, **87**, 132-144.
1913. Die reflexfunktionen des zentral-nervensystems, besonders von standpunkt der rhythmischen Tätigkeiten beim Säugetier Betrachtet. Sonderdruck aus: *Ergebnisse der Physiologie*, Herausgegeben von L. Asher und K. Spiro, XIII, Jahrgang.
1913. (With C. S. SHERRINGTON.) Note on the functions of the cortex cerebri. *J. Physiol.* **46**, xxii.
1913. Rhythmic movement in the mammal. *IX Congres Int. des Physiologistes Groningue*, 2-6 Sept.
1913. (With C. S. SHERRINGTON.) Recovery after lesions of the motor cortex in the anthropoid ape. *IX Congres Int. des Physiologistes Groningue*, 2-6 Sept.
1913. (With C. S. SHERRINGTON.) Reversal in cortical reactions. *IX Congres Int. des Physiologistes Groningue*, 2-6 Sept.
1914. Studies in the physiology of the nervous system. XIV. Immediate and successive effects of compound stimulation in spinal preparations. *Quart. J. Exp. Physiol.* **7**, 197-243.
1914. Studies in the physiology of the nervous system. XV. Immediate reflex phenomena resultant upon compound stimulation in decerebrate preparations. *Quart. J. Exp. Physiol.* **7**, 245-291.
1914. Studies in the physiology of the nervous system. XVI. Decerebrate preparations, successive phenomena in compound reactions—stimuli of synchronous termination and stimuli of asynchronous termination where the extension-reflex is left in action. *Quart. J. Exp. Physiol.* **7**, 293-344.
1914. Studies in the physiology of the nervous system. XVII. Decerebrate preparations, successive phenomena in compound reactions—stimuli of asynchronous termination where the flexion-reflex is left in action. *Quart. J. Exp. Physiol.* **7**, 345-382.
1914. Studies in the physiology of the nervous system. XVIII. The successive effects of the compounding of reflexes where the 'pure' reactions are abnormal (ipsilateral extension or contra-lateral flexion) in decerebrate preparations. *Quart. J. Exp. Physiol.* **7**, 383-405.
1914. Studies in the physiology of the nervous system. XIX. The successive effects of the compounding of reflexes in the 'de-afferented' condition—decerebrate preparations. *Quart. J. Exp. Physiol.* **7**, 407-418.
1914. Studies in the physiology of the nervous system. XX. Rhythmic movements as immediate reflex phenomena of compound stimulation (progression conditioned by antagonistic reflex stimuli). *Quart. J. Exp. Physiol.* **8**, 155-191.
1914. Studies in the physiology of the nervous system. XXI. Rhythmic movements as successive (or terminal) reflex phenomena of compound stimulation (progression conditioned by antagonistic reflex stimuli). *Quart. J. Exp. Physiol.* **8**, 193-288.
1914. On the ordering of reciprocal innervation. *Med. Chron.* September-October.
1914. On the nature of the fundamental activity of the nervous centres; together with an analysis of the conditioning of rhythmic activity in progression, and a theory of the evolution of function in the nervous system. *J. Physiol.* **48**, 18.
1914. The phenomenon of augmentation of excitability in the motor cortex. *J. Physiol.* **48**, xxix.
1914. Motor activation of the post-central gyrus. *J. Physiol.* **48**, xxx.
1914. A respiratory tract in the mid-brain. *Proc. Physiol. Soc.*, May 16: *J. Physiol.* **48**, xxxii.

1914. Note on the functions of the post-central gyrus in the anthropoid ape. *J. Physiol.* **48**, xxxiii.
1915. Studies in the physiology of the nervous system. XXII. On the phenomenon of facilitation. 1. Its occurrence in reactions induced by stimulation of the 'motor' cortex of the cerebrum in monkeys. *Quart. J. Exp. Physiol.* **9**, 81-99.
1915. Studies in the physiology of the nervous system. XXIII. On the phenomenon of facilitation. 2. Its occurrence in response to subliminal cortical stimuli in monkeys. *Quart. J. Exp. Physiol.* **9**, 101-116.
1915. Studies in the physiology of the nervous system. XXIV. On the phenomenon of facilitation. 3. 'Secondary facilitation' and its location in the cortical mechanism itself in monkeys. *Quart. J. Exp. Physiol.* **9**, 117-130.
1915. Studies in the physiology of the nervous system. XXV. On the phenomenon of facilitation. 4. Its occurrence in the subcortical mechanism by the activation of which motor effects are produced on artificial stimulation of the 'motor' cortex. *Quart. J. Exp. Physiol.* **9**, 131-145.
1915. Note on the physiology of the basal ganglia and mid-brain of the anthropoid ape, especially in reference to the act of laughter. *J. Physiol.* **49**, 195.
1915. On the occurrence of a plastic flexer tone in the monkey. *J. Physiol.* **49**, 180.
1915. On the effect of artificial stimulation of the red nucleus in the anthropoid ape. *J. Physiol.* **49**, 185.
1915. On the activities of the central nervous system of the unborn foetus of the cat, with a discussion of the question whether progression (walking, etc.) is a 'learnt' complex. *J. Physiol.* **49**, 208.
1916. Studies in the physiology of the nervous system. XXVI. On the phenomenon of facilitation. 5. Additional note on 'secondary facilitation' in the cortical motor mechanism of monkeys. *Quart. J. Exp. Physiol.* **10**, 97-102.
1916. Studies in the physiology of the nervous system. XXVII. On the phenomenon of facilitation. 6. The motor activation of parts of the cerebral cortex other than those included in the so-called 'motor' areas in monkeys (excitation of the post-central gyrus); with a note on the theory of cortical localization of function. *Quart. J. Exp. Physiol.* **10**, 103-143.
1916. (With R. M. STEWART.) On disturbances of the localization and discrimination of sensations in cases of cerebral lesions, and on the possibility of recovery of these functions after a process of training: (1) Partial recovery of the accuracy of localizing tactile stimuli, together with a discussion of the factors which underlie the process. *Brain*, **39**, 348-454.
1916. Die Reflexfunktionen des Zentralnervensystems, mit Besonderer Berücksichtigung Der Rhythmischen Tätigkeiten Beim Säugetier. II Teil. Sonderabdruck aus: *Ergebnisse der Physiologie*, Herausgegeben von L. Asher und K. Spiro, XV Jahrgang.
1919. (With R. M. STEWART.) Observations on reflex phenomena in cases of spinal injury in man. *J. Roy. Army Med. Corps*, June.
1920. A case of concussion of the spinal cord, resultant on a graze by a live shell: with especial reference to the phenomenon of 'Heteraesthesia'. *J. Neur. & Psychopath.* May, 54-59.
1920. The localization of psychic function in the brain. *J. Neur. & Psychopath.* **1**, 260.
1921. La manifestation graduelle des reactions affectives. *L'Encephale*, April.
1921. A curious physiological phenomenon. *Nature, Lond.* **108**, 529.
1922. Inhibition and excitation in the central nervous system. A preliminary note. *J. Neur. & Psychopath.* **3**, 39.
1922. Instinct and the unconscious. *J. Neur. & Psychopath.* **3**, 98.
1922. The physiology of stepping. *J. Neur. & Psychopath.* **3**, 112.
1922. Reflex orientation of the optical axes and the influence upon it of the cerebral cortex. *Archiv. Neerland. de Physiol.* **7**, 751.
1923. John Berry Haycraft. Obituary notice. *Proc. Roy. Soc. Edinb.* **43**, 264.

1923. Variations in the frequency of stepping produced during concurrent flexion—and extension—reflexes. Proc. XIth Internat. Physiol. Cong., Edinburgh. *Quart. J. Exp. Physiol.* Suppl. Vol. p. 6.
 1923. On the mode of central conduction in reflex activities: is it a direct transmission of nerve impulses, or is there a 'relay' mechanism? *Archiv. Suisses de Neurol. et de Psychiat.* **13**, 138.
 1924. Studies in the physiology of the nervous system. XXVIII. Absence of algebraic equality between the magnitudes of central excitation and effective central inhibition given in the reflex centre of a single limb by the same reflex stimulus. *Quart. J. Exp. Physiol.* **14**, 1-23.
 1925. Cerebral localization of function. *J. Neurol. & Psychopath.* **5**, 359.
 1926. The 'interference' of two flexion reflexes; an examination of Vészi's experiment. *J. Physiol.* **62**, 98.
 1927. The initial phase of reflex inhibitory relaxation in extensor muscles. *J. Physiol.* **63**, 187.
 1927. Review on 'The theory of perception'. *Nature, Lond.* **119**, 773.
 1927. Upon inhibitory relaxations evoked by reflex stimuli of constant intensity acting against varied magnitudes of extensor tone. *J. Physiol.* **63**, 197.
 1927. The end results of the treatment of 'shell shock'. *J. Neurol. & Psychopath.* **8**, 146.
 1927. Absence of a linear relationship between graded simple reflex flexions and the relaxations thereof evoked by a constant extension-producing stimulus. *Proc. Roy. Soc. B*, **102**, 143.
 1927. Absence of a linear relationship between the reflex flexor shortenings evoked by a graded series of flexion-producing stimuli and the 'inhibitory' lengthenings of a constant extension reflex evoked by the same stimuli. *Proc. Roy. Soc. B*, **102**, 150.
 1927. The relation of the magnitudes of remaining reflex shortening in two antagonistic muscles during compound stimulation. *Proc. Roy. Soc. B*, **102**, 159.
 1927. 'Grosshirnhemisphären.' *Handbuch der Normalen und Pathologischen Physiologie.* **10**, 418-524.
 1929. A method for the automatic regulation of the body temperature in decerebrate or spinal preparations in the cat and other animals. *J. Physiol.* **68**, xii.
 1931. Extrapyramidal central mechanisms. Editorial. *J. Neurol. & Psychopath.* **12**, 158.
 1932. A new differential aesthesiometer. *J. Physiol.* **77**, 16P.
- Also—various articles in the *Alpine Journal*.

Books on mountaineering

1944. *Brenva*. London: J. M. Dent & Son Ltd.
1957. (With SIR GAVIN DE BEER.) *First ascent of Mont Blanc*. Oxford Univ. Press.