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Over a period of 35 years Pat Merton was responsible for a succession of elegant experiments, nearly all on human muscle, which elucidated the nervous mechanisms responsible for the control of movement, and the nature of muscle fatigue.

BACKGROUND AND PERSONAL LIFE

Almost everything in Pat Merton’s family history is complicated and colourful, and much of it contributed to his character. His father, Gerald—a pilot in the Royal Flying Corps in World War I, holder of the Military Cross for services in Mesopotamia, and later a distinguished astronomer—was the youngest son of the German portrait painter Hermann Schmiechen, who had a large English clientele, painted two portraits of Madame Blavatsky and was much involved with the theosophists. Schmiechen portraits would later be a striking feature of Pat’s house and also of his college rooms. Pat’s mother, Mary (née Crowley), was from Cork, of Franco-Irish stock, and staunchly Catholic. (Indeed, Mary’s mother had been singing in the Farm Street Jesuit Church choir when a young seminarian who had intended to become a parish priest spotted her, changed his mind, married her and had five children.)

So why the name Merton? Pat’s paternal grandmother Rosalie—whose flattering portrait dominated Pat’s sitting room for much of his adult life—took an interest in her husband’s clients. Among those for whom her husband had painted portraits was the wealthy and philanthropic Zachary Merton (born Zachary Moses) who, with his four brothers, were the leading metal traders in Great Britain and in Germany. By the end of the century, increasingly close relations between Rosalie and Zachary led to a double divorce. Rosalie then married Zachary, and Hermann took the children back to Germany; Gerald had memories of living above a patisserie in Berlin. But within a few years Rosalie was able to bring the children...
back to England, and a few years later Gerald went to Bedales school and then on to Trinity College, Cambridge, to read Natural Sciences. By this time it had become clear that Rosalie was not going to have children by Zachary, and Zachary offered to make her Schmiechen children his heirs if they would change their name to Merton. This they did at the end of Gerald’s first year at Cambridge. Unfortunately, although Zachary kept his promise, much of the money that he left to Rosalie was lost to the family through her infatuation with the theosophists.

It was Rosalie, though, who brought Mary Crowley and Gerald together. Mary acted as her social secretary at Folly Farm, the splendid seventeenth-century Berkshire farmhouse, much extended by Lutyens, that was Rosalie and Zachary’s country home. While in the Royal Flying Corps, Gerald had married, but his wife died of an infection in the second year of the marriage and at the end of the war he came to live at Folly Farm. Here he met and soon married Mary. When Pat was born (in Godalming), the Archbishop of Westminster wrote congratulating Gerald, and said that he would be happy to baptize the child in Westminster Cathedral. Despite this offer (which was not accepted) and despite his largely Catholic schooling—Ampleforth preparatory school, a brief period at the Leys (terminated as soon as his mother realized that it was a Methodist foundation), and Beaumont—Pat as an adult had little sympathy for Catholicism. He did, though, remain on good terms with Monsignor Gilbey, the likeable Catholic chaplain to Cambridge University.

Shortly after the outbreak of World War II, Pat came up to Trinity College, Cambridge, where as a medical student he was exempt from National Service. In those days, medical students read for the Natural Sciences Tripos, and in his third year he specialized in physiology, rather surprisingly getting only an Upper Second. Having graduated BA in 1942, he went on to London to do his clinical work at St Thomas’s Hospital, qualifying MB BChir in 1946. The normal next step for the aspiring doctor would have been to get a job as a house physician or house surgeon, but such jobs were not then essential for getting on the Medical Register. Aiming at a career in research rather than in medical practice—and possibly influenced by his former teacher, William Rushton (FRS 1948), who felt that he had himself been ‘extinguished as a research scientist for about 12 years’ by the study of clinical medicine (Barlow 1986)—Pat eschewed house jobs, and joined Professor E. A. Carmichael’s Medical Research Council Neurological Research Unit in the National Hospital, Queen Square, London. While working there he lived in a flat in 37 Mecklenburgh Square, a house owned by Leonard and Virginia Woolf, and at one time the home of the Hogarth Press, whose discarded signboard Pat retrieved and treasured.

Two or three years after starting at Queen Square, Pat was visiting William Rushton and his wife at Bernard Robinson’s ‘Music Camp’ when he met 20-year-old Gabriel Howe, a drama student and teacher, who was helping with the cooking. She was the daughter of Foster Garfield Howe, a publisher, and of Anna Milhoff, born in Odessa, whose father had emigrated to London with the nihilists and with Kropotkin. In 1951 she and Pat were married; they went off to honeymoon in the Sahara in Pat’s elegant green 1931 Hotchkiss tourer, complete with a spare engine and an ample toolkit.

Such a combination of elegance and technical competence was a recurring feature in Pat’s life. Many years later, wishing to demonstrate to the Royal Society how one’s eyes roll when one’s head is tilted from side to side, he arranged for his subject to sit in a chair that was the bob of a pendulum whose movement was controlled by a giant version of Harrison’s grasshopper escapement.
In 1952 Pat went to Stockholm for two years to work with Ragnar Granit (FRS 1960) in the Neuroscience Department of the Karolinska Institute. He and Gabriel sailed there on a ‘lemmer aak yacht’—a curious Dutch racing barge with lee boards, a high curved prow and a window with leaded lights at the stern—that had originally been acquired by Pat’s father, partly to provide holidays for Pat’s sister, who was crippled by polio. Having arrived in Stockholm harbour they continued to live on the barge, an arrangement that worked well except once when Gabriel, already pregnant with their first child, fell into the harbour—fortunately without ill effect. In 1954 Pat, Gabriel and their new daughter sailed back to London and continued to live on the barge, first in St Katherine’s Dock and later in the Chichester Canal, until Pat bought a large seventeenth-century house in Highgate and embarked on a succession of housing problems that were to extend over the next 12 years.

A bomb had caused one wall of the Highgate house to bulge so that it was no longer a reliable support for the heavy tiled roof. The tiles had to come off and the wall be rebuilt, but before the work was complete Pat was appointed to a lectureship at the Physiological Laboratory in Cambridge. He therefore sold the Highgate house, still under its tarpaulin, and moved. For a few years the family lived in part of a large house belonging to a Cambridge friend, while Pat planned to build. He had always admired an elegant 1938 timber house (now listed by English Heritage as Grade II*) designed by Justin Blanco White for William Rushton, so he approached her explaining that he wanted a house similar in looks but with better sound insulation; it should have a timber exterior but with brick dividing walls and concrete floors. A suitable plan was produced, and a local Cambridge architect was appointed to do some of the detailing and to supervise the construction. This architect’s urge to make changes, though, soon led to his dismissal, and Pat took over as his own site-architect and general contractor—another example of the combination of technical competence and a desire for elegance. And the elegance was not restricted to the architecture. The evening before the long main drain of the house was due for inspection, Pat arrived at my (I.G.’s) nearby house with a sheet of white paper and a pair of Zeiss field glasses. There was a full moon, and by standing in a manhole near the road with his field glasses and getting me to stand in a manhole near the house and reflect moonlight along the drain, he was able to see the silvery trickle running straight and true along the drain’s entire length. It added to Pat’s pleasure that, half a century earlier, the field glasses had been given to his father as a 21st birthday present by a German pilot whom he had just shot down.

It was not until 1966 that Pat and Gabriel, now with three children, moved into their new home, and the building was never quite completed. In particular, the path to the front door was never finished, so access was usually by the kitchen door—approached through a huge carport containing the green Hotchkiss, a black Hotchkiss, a spare engine for the black Hotchkiss, two Bedford vans, a Morris 1000 Estate, a rowing boat, pulleys and tackle from the Dutch barge, a huge trolley-jack, an assortment of ladders, an ancient refrigerator (that had once, in Rosalind Franklin’s mother’s kitchen, stored a sample of polio virus overnight), a brace of deep freezers, and in later years a vast amount of scientific apparatus that would have been thrown out had it remained at Queen Square.

For though after 1957 Pat’s job was in Cambridge, much of his work, particularly his work involving patients, was done with colleagues at ‘the National’. In 1979, the year he became a Fellow of the Royal Society, he was appointed Honorary Consultant in Clinical Neurophysiology there, and in 1981–82 he also held an Honorary Senior Research Fellowship at the Royal Postgraduate Medical School. He became an MD in 1982 and an FRCP in 1991.
In Cambridge he was made a Reader in 1977, and Professor of Human Physiology in 1984. He was a Fellow of Trinity from 1962 until his death.

Both in the Physiological Laboratory and at Trinity, Pat was an inspiring and much-loved teacher, who took endless trouble with his pupils, and with anyone else who needed his help—which could range from drafting a difficult letter for a college servant to providing a mammoth pair of Spencer Wells forceps so that an elderly arthritic Trinity Fellow could put on his own socks.

With an astronomer for a father and a singer for a mother, it is not surprising that Pat had a strong interest in both astronomy and music. The grand piano in his sitting room was usually open—often with the Bach preludes and fugues on the music stand—and a huge loudspeaker in his study was generally playing Bach. There was also a clavichord. In literature his taste was eclectic; he had an encyclopaedic knowledge of the biographies of Lord Rayleigh and of Helmholtz, and he must have been one of the very few scientists who had read both Rashdall’s *Universities of Europe* and Keynes’s *General Theory*. He thoroughly approved of Jane Austen and was totally uninterested in television.

His wide knowledge, his thoughtful nature, his interesting talk and his ready sense of humour made him a splendid companion—provided he liked you. To those he disliked, or for any reason failed to respect, he could be dismissive.

In 1988, after 37 years of marriage, Pat and Gabriel separated, Pat remaining in Cambridge and Gabriel going to the Scottish Borders. Although Pat continued to think intermittently about physiological problems and dined frequently in Trinity, his health gradually declined and he became increasingly reclusive. It was as if the class of people he liked shrank and shrank, and at the age of 79 he took his own life. He is survived by his wife, their son and three daughters, and (including a step-grandchild) nine grandchildren.

**Scientific work**

Pat always maintained that he was inspired by the physiological lectures that were given by E. D. (later Lord) Adrian FRS (PRS 1950–55) when he was a medical student at Cambridge during World War II. He would remark to undergraduates in supervisions that he still referred to his undergraduate lecture notes even 40 years after the event. The lectures may well have been one factor that inspired his fascination with neurophysiology and made him take up a research appointment at the MRC Neurological Research Unit in London in 1946. It is less clear what led him to work on the control of movement, but shortly after arriving there he began work in two fields to which he continued to contribute throughout his career. These were the role of muscle spindles in movement and the causes of muscle fatigue, both of which were flagged by short letters to *Nature* published in 1950 (1, 2)*.

*Muscle spindles and movement: the follow-up servo theory*

Many muscle spindles lie within the main body of almost all skeletal muscles. Each consists of a specially adapted bundle of muscle fibres that are known as ‘intrafusal’ fibres to distinguish them from the main bulk of ‘extrafusal’ fibres in the rest of the muscle. They are innervated by both sensory and motor nerves. The sensory (afferent) nerves send signals to the

* Numbers in this form refer to the bibliography at the end of the text.
spinal cord that provide information about the length of the muscle and the rate at which that length is changing. The motor (efferent) innervation of the spindle is separate from that of the main muscle; activity in these fibres changes the sensitivity of the spindle to changes in muscle length. At the start of the 1950s little was known of the role of the muscle spindle apart from the fact that it participated in the stretch reflex—of which the most familiar example is the tendon jerk. When a tendon is tapped with a hammer it stretches the muscle briefly, causing an increase in the discharge of the spindles in the muscle. This input to the spinal cord causes a sudden brief contraction of the main muscle that we see as the tendon jerk.

Pat’s initial experiments (3) were designed to investigate how the sensory information from muscle spindles was used in normal voluntary movement as opposed to the rather unnatural example of the tendon jerk. At the time, it was well known that if a muscle is contracted voluntarily, an electrical stimulus applied to the muscle nerve produces a synchronized electrical potential (M wave) in the electromyogram (EMG) that is followed by an EMG silence that persists for about 100 milliseconds before resumption of the volitional activity. Several possible explanations of this silence had been proposed. One proposal was that the stimulus causes antidromic activity in motor nerves that leads to refractoriness in the spinal motoneurons. Alternatively, the induced twitch of the muscle could activate afferent activity that could inhibit the ongoing contraction. However, on the basis of experiments in which he had recorded directly the discharge from muscle spindle afferents, B. H. C. (later Sir Bryan) Matthews (FRS 1940) had proposed a third explanation (Matthews 1933). During an electrically stimulated contraction of the muscle, discharge in the spindle afferents paused for a period strikingly similar to that of the silent period. Because muscle spindle afferents were known to activate the stretch reflex, he suggested that it was withdrawal of spindle input during a muscle twitch that led to the EMG silence. He pointed out that spindle input could act as a servo, such that when the muscle was contracted, the spindle discharge could maintain the tension in the muscle via the stretch reflex. When the muscle was stretched, spindle activity would increase and recruit more tension, whereas if the muscle were unloaded, activity would decrease and tension decline.

Pat’s experiments examined the silent period of the human adductor pollicis that is produced during voluntary contraction by an electrical stimulus to the ulnar nerve at the wrist. He showed that the duration of the silent period was highly correlated with the duration of the induced mechanical twitch, which he varied by changing the size of the stimulus and the force of the voluntary contraction. The conclusion was that changes in afferent inflow from the muscle were essential to the silent period. Because silence could be seen (during weak contractions) even with very small superimposed twitches, the role of inhibitory afferents was thought to be small. The results were interpreted as supporting Matthews’s theory of the stretch reflex muscle servo. Indeed, given the delays in the stretch reflex pathway, the pause in spindle discharge must end before the silent period, which is exactly what Matthews had observed.

Pat’s insight in these experiments was to note that the timing of the spindle pause must be carefully controlled to allow for changes in properties of the muscle twitch such as could occur in fatigue. This could be accomplished by adjusting spindle sensitivity by action of the intrafusal efferent fibres. In the initial paper, Pat mentions only that this could explain some pathological variations of the stretch reflex. It was only later that he developed the novel idea that the intrafusal fibres could lead muscle contraction in the follow-up version of the servo theory. In this case, intrafusal activity would adjust spindle discharge and via the stretch reflex...
loop cause a follow-up contraction of the main muscle, in the manner of power-assisted steering on a car.

It is possible that Pat’s understanding of the principles of feedback control that were so important to his theory of the role of muscle spindles was linked to his involvement at that time with the Ratio Club. This was a small informal dining club of young psychologists, physiologists, mathematicians and engineers who met to discuss issues in cybernetics. Contacts with members such as Albert Uttley, a pioneer in artificial neural networks and machine learning, may well have been the source of his more than elementary knowledge of servo systems.

Evidence in support of the follow-up servo had to await Pat’s visit to Granit’s laboratory in Stockholm in 1952–53. There he conducted the only animal experiments of his career and showed that some reflex contractions of hindlimb muscles of the decerebrate cat were preceded by an increase in the discharge from muscle spindles within the same muscle, as would be required of a follow-up servo (4). However, if the cat’s cerebellum was also removed, the spindles were silent, even though some reflex contractions could still be evoked (5). This latter observation indicated the possibility that some muscle contractions could be directly initiated rather than being indirectly driven through the follow-up servo.

All of this work was summarized in an influential review in 1956 (7), in which the terms ‘gamma route’ and ‘alpha route’ were coined to describe muscle contractions that were servo-led through activation of the small gamma fibres to the muscle spindle, and contractions that were due to direct excitation of the alpha fibres to extrafusal muscle. The review also was an important summary of new collaborations that Pat had made with P. H. Hammond and G. G. Sutton. The collaboration with G. G. Sutton concerned the origin of the tremor that can be seen during a voluntary contraction. Sutton’s use of frequency analysis methods showed that this tremor at 8–10Hz was prominent if subjects were attempting to sustain a constant force with respect to a visual feedback signal of their performance. It had been speculated that the tremor was a manifestation of instability in the muscle servo loop, and Pat initially inferred that its modulation by visual feedback was an example of the way in which the sensitivity of the muscle servo was controlled during movements. Later experiments, however, made him change his mind about these effects. Hammond had recorded the EMG responses of voluntarily contracting muscle to stretch, which he found caused an increase in spindle discharge, rather than a decrease as found in the silent-period experiment. There were two features of his results that would crop up 15 years later in the famous series of papers by C. D. Marsden (FRS 1983), Merton and Morton (13). These were that the latency of the main reflex response to stretching a contracting muscle was about twice as long as that of the spinal monosynaptic stretch reflex. The second feature was that the reflex magnitude was controllable by the intent of the subject, being larger if the subject was instructed to contract on perceiving the perturbation and smaller if instructed to allow it to occur. The combination led Pat to suggest that there might be a stretch reflex pathway through the brain in addition to the well-known spinal stretch reflex.

The precise pathway responsible for the long latency of the stretch response in contracting muscle was first suggested in 1968 by C. G. Phillips FRS (Phillips 1969). Recognizing the importance of the direct corticospinal projection from cerebral motor cortex to spinal cord, and the recently discovered projection of muscle spindle afferents to sensory cortex, Phillips raised the possibility that there might be a ‘transcortical’ stretch reflex in addition to the monosynaptic spinal pathway. This was brilliantly exploited by Pat in a long collaboration with C. D. Marsden and H. B. Morton in the late 1960s to the mid-1980s. By that time, Pat had moved to take up his position in the Physiological Laboratory in Cambridge, but all of the ‘3M’s’ exper-
periments were conducted back in London at the National Hospital in Queen Square, where Pat had begun his career.

H. B. Morton was an ex-radar engineer who had an extraordinary talent for building, and later for programming, novel pieces of neurophysiological equipment. With Pat, he used brushless servo motors to produce very carefully controlled perturbations of muscle contraction during voluntary movements. The experiments were a direct extension of Hammond’s original observations in the 1950s, but the equipment, and the ability by 1970 to average the EMG responses rather than optically superimposing individual response traces, created a leap forward in analysis. C. D. Marsden was at that time a young and brilliant neurologist who had begun with a shared interest in tremor, but then provided much of the neurological data that supported the experiments in healthy subjects.

The papers that emerged provided the first evidence for a transcortical stretch reflex in humans. They showed that the latency of the response was compatible with a pathway via the motor cortex (15, 16) and that it was absent in neurological patients who had lesions within the pathway (17, 18). The ability to control the stretch carefully also allowed Pat and his colleagues to show that a stretch reflex occurred if they halted an isometric muscle contraction. Because the main muscle had not actually been stretched, this was evidence that muscle spindles had continued to contract during the halt and that the increase in their discharge had recruited additional EMG activity. It is interesting to note that these papers continued to refer to a muscle servo system, even though the follow-up servo idea was under question from microneurographic recordings that showed that sensory discharges from human muscle spindles did not increase before the onset of volitional muscle contraction, unlike the situation described during reflex contractions by Eldred, Granit and Merton in the decerebrate cat (4). However, the reflex increase in EMG activity that Marsden, Merton and Morton observed during the halt led them to conclude that volitional contractions were not simply the result of ‘alpha’ activation alone (13). It was more likely that there was coactivation of alpha and gamma systems so that the spindles were continually adjusted to be able to detect either loading or unloading of muscle force. Recent work suggests that the spindles are in fact activated more than the extrafusal muscle and that their rising discharge with increasing contraction force assists in recruiting muscle force via the stretch reflex servo (Hagbarth 1993). Thus, although Merton’s original idea of a follow-up device may be incorrect, servo action undoubtedly occurs.

The last papers on stretch reflexes addressed the unexpected finding that stretch to one muscle sometimes evokes reflex responses in distant muscles (20). These distant responses occur in postural muscles that are supporting the contraction, such as the leg muscles in a standing subject when a tug is given to the arm. The perturbation stretches muscles in the arm, and will eventually cause a small sway of the whole body, yet the reflex occurs in the leg before the body begins to sway. The responses were therefore termed anticipatory postural responses to indicate a role in suppressing perturbations that were about to occur. They were thought to involve a transcortical reflex pathway.

**Muscle fatigue**

Pat’s first papers on fatigue appeared at the same time as those on the silent period (1, 6, 8). They address the simple question of whether the loss of strength that occurs during a voluntary contraction is due to failure in the contractile process of muscle or to failure of the central nervous system to activate the muscle. In other words, is the fatigue peripheral or central in
origin? The answer to the question depends critically on measuring whether electrical stimulation of a fatigued muscle via its nerve can produce more force than was possible voluntarily. With characteristic ingenuity, Pat developed a device for measuring the force applied by the adductor pollicis muscle during adduction of the thumb. The data very clearly showed that, at least for this muscle, fatigue during a maximum sustained contraction was of peripheral origin. In addition, Pat introduced the technique of ‘twitch interpolation’ to estimate the level of voluntary contraction. If an electrical stimulus is given to a muscle nerve during a truly maximum contraction, the extra discharge of motor units cannot generate any additional force. However, if the contraction is less than maximum, the stimulus generates a superimposed muscle twitch whose amplitude is approximately proportional to the contraction, expressed in percentage maximum. The technique is still in regular use, although curiously as a way of estimating central fatigue rather than a way of proving that it does not occur (Gandevia 2001).

The work led Pat to question the nature of the peripheral fatigue. If a muscle was fatigued so that it was no longer able to exert any force, electrical stimulation of the muscle nerve could still evoke an action potential in the muscle that was only marginally smaller than normal. This indicates that fatigue of neuromuscular transmission contributes little to contraction failure. He speculated that if it were possible, with a large enough electrical impulse, to stimulate the membrane of the muscle fibres directly and elicit muscle action potentials directly, then the action potentials should be unaffected by exhaustive fatigue. He mentions attempting to do this in the early papers (8), but returned to the topic later in collaboration with R. H. T. Edwards and developed a high-voltage stimulator that could do this (21). However, its main use turned out to be not to stimulate muscle but to stimulate the brain (see below).

Pat also was intrigued by an observation of Naess & Storm-Mathison (1955) that high-frequency electrical stimulation of muscle during a maximum voluntary effort caused the force to decline more rapidly. This led him to speculate that during volitional maximal contractions, the muscle was activated at lower rates of innervation than had been applied electrically. In 1968 he came back to this problem in collaboration with C. D. Marsden and J. C. Meadows and demonstrated that maximum muscle contraction produced by high-frequency stimulation of the muscle nerve could only be maintained for as long as a volitional effort if the pattern of stimulation started at a high frequency and then declined (22). They also made use of the fact that in some subjects, adductor pollicis sometimes receives a minimal innervation from the median rather than the ulnar nerve (the Martin–Gruber anastomosis). After transmission in the ulnar nerve had been blocked with local anaesthetic, it was possible to observe a similar reduction in the discharge rate of single motor units innervated by the median nerve during an attempted maximum contraction. Pat and his colleagues proposed that fatigue develops on the basis of the number of impulses discharged rather than the duration of the contraction, and referred to the gradual slowing of discharge rates during fatigue as ‘muscular wisdom’. Later work by others showed that the duration of the force response of a single motor unit increases during fatigue, so that the same tetanic force can be developed at a lower innervation frequency.

Other observations

Although he wrote few papers on the topic, one of the most contentious of Pat’s opinions was that signals from muscle spindles do not reach consciousness. This began after spindles had been described in the extraocular muscles. Pat knew that imposed movements of the eyeball in the dark do not give any sense of movement, and using local anaesthesia of the conjunctiva...
to abolish sensation from the eyeball itself, he demonstrated this in a series of experiments with G. S. Brindley (FRS 1965) that were later filmed by the BBC (11). Later, they used ischaemic anaesthesia of the hand with a sphygmomanometer cuff around the wrist to remove sensation from cutaneous and joint receptors in the thumb and fingers while leaving many of the muscles that move the digits intact in the forearm. Under those conditions, movement of the fingers produced no sensations even though the muscle spindles must necessarily have been activated. They concluded that spindle inputs do not reach consciousness. Unfortunately the data are not quite as clear cut as was made out. Later experiments by others show that at least some spindle input reaches consciousness.

Films also exist of Pat’s demonstration of torsional eye movements (9, 10). Until the mid-1950s it had only been possible to investigate the slow movements that compensate for side–side movements of the head. Pat developed a swing seat that rotated about the axis of one eye so that he could observe torsional movement without accompanying movement of the eyeball. Quick rotations of the chair produced torsional saccades, and continuous rotation led to torsional nystagmus. He returned to eye movements several times. Shortly after he moved to Cambridge he showed that the accuracy of moving the eyes in the dark was similar to that of moving the arm and hand (12). His method of measuring the position of the eye in the dark was typically ingenious: he used the afterimage from a brief powerful flash of light projected through a small aperture. If the subject was fixating the aperture at the end of the eye movement, then the afterimage was at the fixation point, whereas if the subject was fixating, say 2° to the right, then the afterimage was 2° to the left of fixation. The position of the fixation point relative to the aperture at the time of the flash could be determined subsequently by fixating the zero of a marked scale and then having the subject read off the apparent position of the afterimage. He later turned to the phenomenon of saccadic suppression of vision in collaboration with L. A. Riggs and H. B. Morton (14). They showed that phosphenes elicited by electrical stimulation of the retina had a higher threshold when timed to occur during a saccade. This was evidence that a substantial proportion of saccadic suppression of vision was neural rather than caused by optical blurring when the image passes rapidly over the retina.

One of Pat’s final contributions is still being exploited. He had been trying for some years to develop an electrical stimulator that could activate muscle fibres directly rather than via the neuromuscular junction. One design that seemed to work used a high-voltage capacitative discharge. For reasons that are not clear, he then tried out the same stimulator on his own head in an attempt to activate the motor cortex through the skull and scalp (19). On the first occasion it was successful and produced a visible twitch of the muscles of the contralateral hand. Stimuli applied to the visual cortex yielded phosphenes and he proved that these were not due to spread of stimulus to the retina (which is very sensitive to electrical stimuli) by ischaemic anaesthesia of the eyeball, a rather dangerous and unpleasant technique. At first the method was pursued only by enthusiastic physiologists because the stimulus also causes a contraction of scalp muscles and local discomfort at the site of stimulation. However, a development of this, transcranial magnetic stimulation (Barker et al. 1985), in which a magnetic field is used to carry the electrical stimulus across the high resistance of the skull and scalp, is painless and in routine use in very many centres.
ACKNOWLEDGEMENTS

We are particularly grateful to Gabriel Merton for helping us sort out Pat’s complicated family history and for a wealth of detail about his life, and to Horace Barlow FRS for comments about our account of Pat’s scientific work.

The frontispiece photograph is a copy of a photograph in Trinity College library thought to have been taken in the 1960s.

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