''THE QUEEN HAS BEEN DREADFULLY SHOCKED'': ASPECTS OF TEACHING EXPERIMENTAL PHYSIOLOGY USING ANIMALS IN BRITAIN, 1876–1986

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Animal experimentation has been subject to legislative control in the United Kingdom since 1876. This paper reviews the impact of that legislation, which was replaced in 1986, on the teaching of practical physiology to undergraduate students. Highlights and case studies are also presented, drawing on Government reports and statistics, published books and papers, and unpublished archival data.

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The use of experimental animals in medical research and teaching arouses concern and discussion in countries around the world. It is not the intention here to discuss or enter the ethical debates that surround the issue but to provide a historical perspective, focused on Britain, on the use of animals in the teaching of physiology from 1876 until 1986. In the United Kingdom, these matters first came to public attention in the 1870s, when legislation, the Cruelty to Animals Act, was enacted to regulate the conduct and conditions of animal experimentation. This was the first such legislation in the world, and it remained on the Statute Books, with some modifications, until 1986, when it was replaced with the Animals (Scientific Procedures) Act. The 1876 Act defined the conditions under which experimental physiology could grow—individual researchers and teachers had to satisfy a system of licensing and certification requirements, and the laboratories in which they worked had to be registered with the Home Office and were subject to random unannounced inspection by Government officials. It is within that framework that this analysis of the use of animals in the teaching of physiology in the United Kingdom has been undertaken.

The chronological range of this paper is clearly dictated by the relevant legislation, from 1876 until 1986. From the very beginning the law required that each licensee had to make an annual report, the so-called annual return, to the Home Office detailing his activities under the Act; all these data were then concatenated into an Annual Report, presented by the Home Secretary to Parliament, and subsequently published as an official government record. Thus there is an immense statistical database that has been utilized in studying the use of experimental animals in the United Kingdom. Additionally, a variety of sources have been consulted, including the official reports of various Royal Commissions established during the period, those into the working of the 1876 Act and also those on medical education, in addition to textbooks, practical manuals, and laboratory schedules, notes and reports written by students, and other unpublished laboratory records.

The educational focus will be exclusively on undergraduate teaching, which can usefully be subdivided into ''junior'' students, either those seeking medical qualification or science students for whom physiology is only one component of their degree studies, and

''senior'' students, so-called ''intercalated'' medical students undertaking an additional year of specialized training during the course of their medical studies, and final-year undergraduates specializing in physiology. Until after the Second World War the vast majority of undergraduate students taking physiology courses in the UK were ''junior'' medical students, and it is mainly since the 1950s that the numbers of intercalated medical students and science students have grown substantially. As the numbers of these senior students increased, their educational requirements were recognized to be somewhat different from those of the junior students. Gradually, from the 1950s onwards, these two groups have become quite distinct as far as the teaching of practical physiology is concerned. Junior students are usually required to perform simple practical procedures themselves, more complex experiments being demonstrated to them by a lecturer, whereas the senior students often carry out more extensive experimental investigations themselves, albeit under close supervision. As such, the activities of these latter students merge with those of postgraduate students, but it has proved almost impossible to assess the activities of postgraduates as an identified group because they cannot be adequately distinguished in official records from their supervisors and other professional medical scientists.

Throughout the first 80 years under review, student numbers grew gradually. The major growth spurt occurred after 1950, when the higher education sector in Britain expanded enormously, especially during the 1960s—which saw increasing numbers of students, enlarged departments, and new universities. It is difficult from official records to determine precisely how many students were studying physiology at any one time. This is because physiology was rarely classified as an independent subject, frequently being subsumed under the expressions ''life sciences'' or ''natural sciences'' or being listed, variously and inconsistently, in association with anatomy, biochemistry, or pharmacology. Table 1 provides some indication of the beginning of this growth period, taken from Government statistics at times when physiology was unequivocally, and independently, categorized.

TABLE 1
Full-time students in British universities studying medicine, physiology, or physiology with another subject, usually pharmacology, during the 1950s and 1960s (Ref. 26)

	Medical Students	Physiology	Physiology+
1950	1,047	76	14
1955	2,032	124	3
1960	2,400	202	23

THE 1870S—THE GROWTH OF PHYSIOLOGY AND THE CONTROL OF PHYSIOLOGISTS

The 1870s were auspicious years for British physiology, as new ideas from the Continent infiltrated into medical practice, research, and teaching. Among others, Claude Bernard (1813–1878) in Paris and Carl Ludwig (1816–1895) in Leipzig had taught new techniques of experimental physiology, a shift of emphasis from the morphological study of dead material to the study of the function of living animals and their tissues and organs, in vivo and in vitro. Men influenced by these new methods became significant in the professionalization of physiology in Britain, as they occupied newly created academic positions, wrote books, laboratory manuals, and articles espousing the new physiology, and introduced practical classes using animals, all of which consolidated and perpetuated that experimental approach. ''Physiology'' was emerging in three separate but related divisions: histology, chemical physiology, which later gave rise to biochemistry, and experimental or practical physiology. At the beginning of the decade, the Royal College of Surgeons of England insisted that students attend a course of *practical* physiology as a requisite for their license, without which no man could qualify for surgical practice. This was a significant advance for the discipline and confirmed its place in medical education.

Institutionally and professionally, the subject was also advancing, spearheaded by three men from University College London. All had been trained in, or influenced by, the new Continental physiology and all soon occupied influential positions from which to further promote and shape physiological research and teaching in Britain. In 1870 Michael Foster left University College London to become the first Praelector in Physiology at Trinity College Cambridge and, 13 years later, the first Professor of Physiology of Cambridge University; John Burdon Sanderson became Professor of Physiology at University College London in 1874 and was created the first Professor of Physiology at Oxford in 1882; Edward Schäfer (later Sharpey-Schafer) succeeded Sanderson at University College

London until becoming Professor of Physiology at Edinburgh in 1899 (7).

The explicit use of experimental animals in this new, practical physiology aroused indignation and concern among the lay public, and vociferous antivivisectionist activity grew (6). The year 1874 had been the Jubilee year of the Royal Society for the Prevention of Cruelty to Animals, and during the accompanying celebrations, Queen Victoria's well-known personal anxieties about the suffering of experimental animals had been publicly conveyed to the Society's President. The following year, in 1875, the Society for the Protection of Animals Liable to Vivisection (later the Victoria Street Society, later still the National Anti-Vivisection League) was founded, and again Queen Victoria's repugnance for animal experiments and the teaching of them to students was further expressed in a letter to Joseph [later Lord] Lister, then Professor of Surgery at Edinburgh and Surgeon to the Queen, written by her private secretary, ''The Queen has been dreadfully shocked at the details of some of these practices, and is most anxious to put a stop to them.'' The Queen, as did many of her subjects, expressed particular concern about ''encouraging students to experiment on dumb creatures'' (9). Lister defended the practice to the Queen, in his response stressing the humane feelings of the medical profession and their avoidance of the deliberate infliction of pain.

In 1875 Lister was able to amplify his statements to a larger and more public audience when, in the midst of and in response to, antivivisectionist outcry, the Government appointed a Royal Commission to inquire into ''The Practice of Subjecting Live Animals to Experiments for Scientific Purposes.'' Witnesses from the then tiny physiological community and also from the larger body of the medical profession emphasized the need for Britain to establish research schools of physiology in which students could be taught the new experimental science. Lister strongly supported the Royal College of Surgeons' position of teaching practical physiology to students, emphasizing to the Commission, as he had done to the Queen, that information and insights not available from ''mere'' lectures came from the experience of performing original observations. Other witnesses to the Royal Commission included a wide range of medical opinion and antivivisectionist campaigners, in addition to other prominent members of Victorian society, including the clergy. The few physiologists then engaged in teaching were closely questioned about their practical courses: John Burdon Sanderson described that offered at University College London, consisting of histology taught by Edward Schäfer, classes on chemical physiology that did not involve animals, and a course of experimental physiology in which a number of pithed frogs and five or six rabbits, under complete anesthesia, were used for observations and experiments.

In particular, however, the Royal Commissioners called for questioning the four authors of the *Handbook for the Physiological Laboratory*, published in 1873. This was a practical guide to the new physiology, heavily dependent on experimental investigations using living animals, with chapters written by Emanuel Klein, John Burdon Sanderson, Michael Foster, and Thomas Lauder Brunton (13). The book posed two problems—it was addressed to the ''beginner'' in physiology, although the status of such a ''beginner'' was never defined, and throughout the text only sporadic mention was made of the need to use anesthetics, a matter immediately commented upon by the book's reviewers and seized upon by antivivisectionists. John Burdon Sanderson stressed to the Commission that by ''beginner'' he meant to refer to a senior student, often already medically qualified, working under the direction of a skilled physiologist in a research laboratory. The inference that an inexperienced and unsupervised student was expected to carry out the manipulations and procedures was incorrect. But it was the question of the use of anesthetics that was to be central to the conduct and recommendations of the Royal Commission, and the lack of clear instructions about such matters in the *Handbook* concerned the Commissioners greatly. Some witnesses argued that it was because anesthetics were routinely used that no explicit mention had been made of them and that contemporary books, such as that based on the course offered at Edinburgh University, were similarly inconsistent about mentioning the use of anesthetics (1). All the witnesses agreed, however, that it was an unfortunate oversight. But the testimony of one of the *Handbook*'s authors, Emanuel Klein, an Austria-born bacteriologist, was to prove decisive. He admitted that many of the experiments he described in the *Handbook* were painful and that he used anesthetics only for his own convenience, to

prevent being scratched or bitten by a pain-raged animal. In response to several further questions, he repeated his view and volunteered the information that he gave no thought to the feelings of the animals. The die was cast—the Royal Commission, widely believed, before Klein's evidence, to have been unlikely to propose any legislative interference, recommended a series of restrictive measures, including a total ban on experiments on cats, dogs, horses, mules, and asses (19).

After these recommendations, strong representations were made by several sections of the medical profession during the latter part of 1875 and early 1876 to reverse this prohibition. The General Medical Council and the British Medical Association organized a petition for readers to sign in the *British Medical Journal* against these exclusions. This appeal eventually achieved limited success, because a series of additional certificate requirements was introduced that provided these particular animals with additional protection (see below). Others, more directly concerned with the advocacy of the new physiology, responded to a letter from John Burdon Sanderson, in which he invited colleagues to ''form an Association of Physiologists for mutual benefit and protection'' in the light of the Royal Commission's recommendations and the likely impact they would have on the research and teaching work physiologists wished to promulgate. The response to this invitation initiated the beginning of the Physiological Society, thus created as a direct consequence of animal experimentation legislation, which became and remains the professional organization of physiologists in Britain (22).

THE CRUELTY TO ANIMALS ACT 1876 AND CERTIFICATES FOR TEACHING

In August 1876 the modified recommendations of the Royal Commission became law as the Cruelty to Animals Act. This was an enabling act, that is, it permitted people to perform actions for which they would otherwise be prosecuted, and it allowed for ''the advancement by new discovery of physiological knowledge'' by experiments ''calculated to give pain'' on nonhuman vertebrates, although the word experiment was never legally defined, an omission that was to cause some difficulties in later years (24). The operational conditions were quite stringent: premises had to be registered with the Home Office; each individual was personally licensed by the Home Office; an additional system of certificates permitted specific kinds of experiments; and each individual had to provide an annual account of his work to the Home Secretary. Anyone granted a license, for which he needed recommendations from two named authorities, could perform nonrecovery experiments under complete anesthesia; and the supplementary certificates, summarized in Table 2, permitted a range of more specialized work.

As far as teaching was concerned, the Act posed immediate problems. There was no explicit provision for educational activities, and the only obvious way in which a student could perform work was by being personally licensed. This would clearly have been inappropriate for junior students, and no evidence has been found in the official records that such permission was ever sought. It was only from the late 1950s onwards, when the numbers of senior students, the intercalated medical students and Honors science students studying physiology started to increase, that the Home Office regularly granted ''student'' licenses, under strict supervision conditions, to a limited number of senior undergraduates to undertake research projects.

In what way did the requirements and conditions of the 1876 Act affect the teaching of physiology? That is an almost impossible question to answer—experimen-

TABLE 2
Summary of certificate applicability under the 1876 Cruelty to Animals Act

Certificate A	Permitted work without the use of anesthetics; used to cover simple inoculations, venesection, and feeding experiments
Certificate B	Experiments using anesthesia for part of the time, i.e., for recovery surgery, plus regulations about aseptic procedures during surgery and the aftercare of wounds
Certificate C	For demonstrations to approved professional audiences
Certificate D	For the demonstration of already known facts
Certificate E	An additional certificate needed for any kind of research on cats or dogs; in 1893 it was subdivided: Certificate E to accompany Certificate A and Certificate EE to accompany Certificate B
Certificate F	In conjunction with Certificate A or B, was needed for experiments on horses, asses, or mules

tal physiology was in its infancy in the 1870s, and there was little extant teaching involving animals; evidence presented to the 1875 Royal Commission by teachers such as Burdon Sanderson suggested that few animals were used, and they were either pithed (frogs) or fully anesthetized (mammals). But from 1876 onwards it was possible for a properly licensed scientist, working in registered premises, to demonstrate experiments, if he also held Certificate C, which allowed for demonstrations as illustrations of lectures before a professional audience or to bona fide students, demonstrations to nonprofessional audiences being strictly forbidden. The legal restrictions of the certificate meant that the demonstration had to be for the acquisition of knowledge and the animals had to be completely anesthetized throughout and killed immediately afterwards. Additionally, there was Certificate D, which provided for ''the verification of already known facts.'' What that meant has never been determined, and few physiologists ever applied to hold it, many arguing that any procedure on a living animal was a potential experiment from which previously unknown facts might emerge.

Figure 1 shows how many experiments were performed under the authority of these two certificates during the 110 years of the Act, taken from the published Annual Reports made every year by the Home Secretary to Parliament. Certificate C returns are indicated by the continuous line, with a change of scale in 1930, and the asterisk marks the only occasion experiments performed under the authority of Certificate D were reported. Few such D certificates were ever held: for the years from 1877–1880 Professor William Rutherford of Edinburgh and his assistant, Dr. John Gibson, both held them, although only Gibson ever reported any work (the asterisked point in Fig. 1), Dr. McGill of the Army Medical School in Netley held a certificate during 1877, J. Macpherson of Edinburgh held a certificate in 1891, and William Rutherford again held such a certificate from 1892–1899, although no work was reported under their authority. From 1899 there was no longer a holder of Certificate D, although it continued to be included in the Annual Reports made by the Home Secretary to Parliament until the beginning of the First World War. Its existence seems to have been entirely forgotten by the Home Office, and indeed in 1963 when the Littlewood Committee met to consider ''Experiments on Animals,'' it was firmly stated that ''there is no record of this certificate [D] ever having been used'' (12).

In contrast, the continued use of Certificate C throughout the period of the Act confirms its utility, because it was used increasingly frequently by licensed experimenters. It must be remembered that the data included in Fig. 1 are from *all* demonstrations, including those to professional societies, etc., in addition to those for undergraduate teaching. These data will

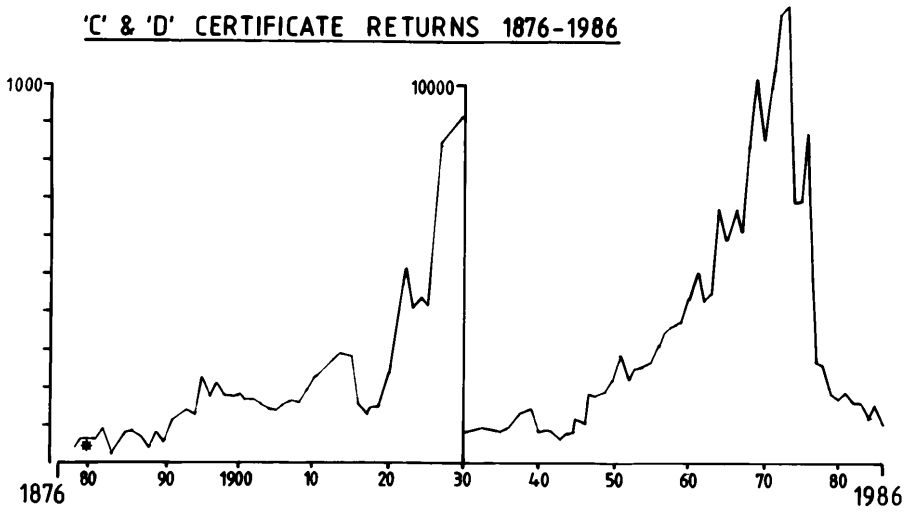

FIG. 1.
Numbers of experiments reported under the authority of Certificates C and D from 1876–1986. *Experiments under authority of Certificate D.

also include returns by other than physiologists, for example, professional and class demonstrations by pharmacologists, although the work will be essentially physiological in nature and it is reasonable to assume that the bulk of these returns is for teaching. Until the early 1970s there is a gradual increase in the numbers of such demonstrations reported—which is also true for all other parameters associated with the Act, because the numbers of licensees, registered premises, and experiments all increased during the 110 years under review. At the beginning of the period, the returns under Certificate C accounted for about 25% of the total numbers of experiments performed. By 1890 they were less than 3% of the total; 20 years later they formed less than 1% of all experiments, and they remained below that level until 1986.

Two obvious dips in the graph, from 1915 to 1918 and from 1941 to 1945, are readily attributed to the influence of the two world wars, and the continuing rise during the 1950s and 1960s reflects the growth of University education. The peak usage of Certificate C occurred in 1973, when 12,000 demonstrations were reported; this was followed by a very marked decline, which may be related to a number of factors. Clearly, external opposition and internal dissent at the use of animals in general had some effect—not least in that many animal users may have genuinely sought to decrease the numbers of animals they used. The increased availability of alternatives such as videos and computer simulations may also have reduced the numbers of animals used, and it was increasingly realized that such techniques were often more economical in time and money—spending a few days planning and filming a video that can be used on many occasions compared with organizing a demanding, regular series of large-scale animal practical classes. A consequence of these reductions has been that as fewer students have been trained with direct, hands-on experience of animal work, gradually the pool of relevant expertise among demonstrators and academic staff has decreased, and practical classes using animals have further declined. Finally, there have been shifts within the discipline itself, particularly well illustrated by the increased use of human subjects and the frequent insistence by educational authorities that they are the only relevant animals for study by medical students (see below).

LIBEL AND LAW BREAKING: THE BROWN DOG AFFAIR OF 1903

A physiological demonstration to medical students became national news in 1903, when the physiologist William Bayliss was accused of cruelty in a book published by the National Anti-Vivisection Society. The demonstration, of pancreatic secretion in an anesthetized dog, took place in the Physiology Department of University College London on February 2nd, and the class was infiltrated by two Swedish antivivisectionists, Liesa von Schartau and Louisa Lind-af-Hageby. They published an account of the procedure claiming that the animal was not anesthetized and had struggled during the experiment, and they accused the demonstrator, Bayliss, of behaving cruelly and illegally. Bayliss issued a writ for libel against the publisher, the Honorable Stephen Coleridge, and the case went to court. The future Nobel laureate Henry Dale, then a student assistant working on pancreatic secretion, had helped Bayliss at the original demonstration and was called as a witness. Dale's evidence in court described the demonstration and confirmed that the dog, moribund from anesthetics, was passed to him to kill and remove the pancreas several hours after the demonstration began. The two Swedish women maintained vigorously that the dog had not been anesthetized and suggested that its vocal cords had been cut to prevent it crying out. Their defense collapsed under questioning, and Bayliss won his libel case. He was awarded £2,000 in damages and used the money to endow a Scholarship in physiology at University College London (4).

This so-called ''Brown Dog'' affair led to clashes between medical students and police on the streets of central London when the International Anti-Vivisectionist Council erected a memorial to the animal in Battersea, South London. The statue was inscribed, ''In memory of the brown terrier dog done to death in the laboratories of University College London in February after having endured vivisections extending over more than two months and having been handed from one vivisector to another until death came to his release.'' Demonstrations by medical students against the monument, during which damage was caused to the statue, led to several of them being arrested, appearing before local magistrates, and being fined for unruly behavior. This treatment of their fellow protest-

ers engendered further demonstrations, as *The Times* for 1907 reported ''hundreds of University students'' marched down the Strand in London to burn an effigy of the magistrate; when it failed to ignite, they threw it into the Thames.

1906–1912: SECOND ROYAL COMMISSION

Continuing unrest, public demonstrations, and the activities of antivivisectionists, which included press, poster, and handbill campaigns on the streets of London and antivivisectionist ''shops'' with lurid displays including stuffed animals with gags in their mouths, led to the establishment in 1906 of a second Royal Commission to examine the working of the law. The dominant focus of the inquiries was to evaluate the ways in which the law was administered and to examine its shortcomings. Physiologists who had been particularly concerned about restrictions on research had, in 1884, established the Association for the Advancement of Medicine by Research (AAMR), an informal advisory group that offered the Home Office guidance about the granting of licenses and certificates and served as an organization to protect licensees, to watch Parliamentary proceedings for further moves to restrict animal experimentation, and to educate medical men in general on the importance of animal experiments. It was the AAMR that provided and coordinated the presentation of a considerable amount of evidence to the Royal Commission, on behalf of the medical community, and their predominant concerns were with the regulation of research activities. Matters relating to teaching were regarded as consequent upon research activities and received little explicit attention.

That is not to say that teaching was completely ignored. The Commissioners did question several witnesses about their current practices: Ernest Starling, the head of the department of physiology at University College London, where the ''Brown Dog'' affair had occurred, estimated that he gave between 8 and 12 demonstrations a year to his senior class, each on a single anesthetized animal, often a dog. On the whole, however, teaching was not a major issue for the Royal Commission, and with respect to the question of demonstrations their final report concluded ''we think that the provisions of the present Act are sufficient'' (20). The major pleas for change came from surgeons who wanted students to be allowed to use animals to practice on to acquire manual dexterity. This was a matter on which the 1875 Royal Commission had determined views, and the practice had not been allowed; indeed, there had been little debate at the time. Between 1906 and 1912 an array of contradictory evidence was presented on the matter, some witnesses arguing strongly that not only was the acquisition of manual skill in this way justified, it was an essential use of animals. Despite these opinions, the restriction remained in force throughout the life of the Act (20). By and large the second Royal Commission endorsed the status quo and expressed satisfaction with the operation of the law, its major recommendation being to establish a Home Office Advisory Committee to continue to monitor the working of the Act. The question of manual dexterity training was considered again in 1965 when the Littlewood Committee on Experiments on Animals met. Representatives from the Universities Federation for Animal Welfare and the Research Defence Society both objected to the ''practice, which is believed to exist in some foreign countries, of requiring students of surgery to practise a series of major operations on each of a number of animals which are kept alive as long as they can be made to last out,'' and the Committee once again endorsed the prohibition of the 1876 Act on using animals for this kind of training (12).

While the second Commission was sitting, a major critic of the influence of the Act on the teaching of physiology emerged. This was an outside observer, the American Abraham Flexner, who, in his 1912 report on German, French, and British medical education, reserved particular scorn for what he termed ''the obscurantist anti-vivisectionist legislation,'' which he considered a serious handicap to the teaching of physiology in Britain (5). His criticism, however, was tempered by admiration for the organization of practical teaching in Britain, and he quoted from Charles Dickens' novel *Nicholas Nickleby* in his report on physiology, ''[t]o the English belongs the credit of devising a sound method of undergraduate scientific instruction.... The national instinct must be fundamentally sound; for the head of Dotheboys Hall was already on the right track. 'We go upon the practical mode of teaching,' explained Mr Squeers to Nicholas Nickleby. 'C-l-e-a-n, clean, verb active, to make bright, to scour; W-i-n-d-e-r, winder, a casement. When the boy knows this out of book, he goes and does it.' The

essential features of undergraduate instruction are these: the demonstrative lecture and the practical work run side by side.'' Flexner singled out the classes run at University College London under the direction of Ernest Starling, those at Guy's Hospital under Marcus Pembrey, and those at Cambridge under J. N. Langley for especial praise, comparing them most favorably with the French and German systems of mass demonstrations, which he considered to be useless ''deceits.'' Flexner appears not to have considered whether the requirements of the Act that insisted on good laboratory working practices, including appropriate and adequate anesthesia and properly trained and licensed demonstrators, had any direct bearing on the satisfactory state of affairs he reported.

POST-FIRST WORLD WAR

Much of the antivivisection furor exhibited at the second Royal Commission died down during the First World War, although some of it was channeled into antivaccination campaigns. During this period, too, medical education was reviewed by the General Medical Council, the licensing and regulatory body of British medicine, in view of increased wartime requirements for qualified medical practitioners. Some courses were curtailed, and inevitably this seems to have led to a reduction in the scientific training component of the undergraduate course (see also the data from Bristol University, Fig. 2).

Immediately after the First World War, reconstruction and development was most marked in medical research, as the Medical Research Committee [later reconstituted as the Medical Research Council (MRC)], which had been founded in 1913 but whose activities had been diverted by wartime necessities, began to function efficiently. The establishment by the MRC of its own independent research facility, the National Institute for Medical Research, modeled to a large extent on the Rockefeller Institute, heralded a level of professionalization of medical research that occupied antivivisectionist protest for many years to come (25).

Educational concerns came to the fore in November 1926, when there was a highly publicized, and successful, prosecution of a dealer who had supplied two stolen dogs to the Institute of Physiology of University College London. The Professor of Physiology, Charles Lovatt Evans, had acquired the animals in good faith but recognized that animal supply difficulties left physiologists such as himself in a vulnerable position (the use of pound animals, as in the United States, has never been permitted in Britain—unclaimed strays were and are destroyed). The case provoked a flurry of publicity in the national and medical press and finally confirmed the lurid horrors of ''pet stealing'' that antivivisectionists had warned of for years. The matter was immediately raised in the House of Commons, and an orchestrated campaign against animal experimentation, especially the use of dogs, was initiated. Throughout the 1930s frequent legal attempts were made to prevent the experimental use of dogs, although these were consistently unsuccessful (25).

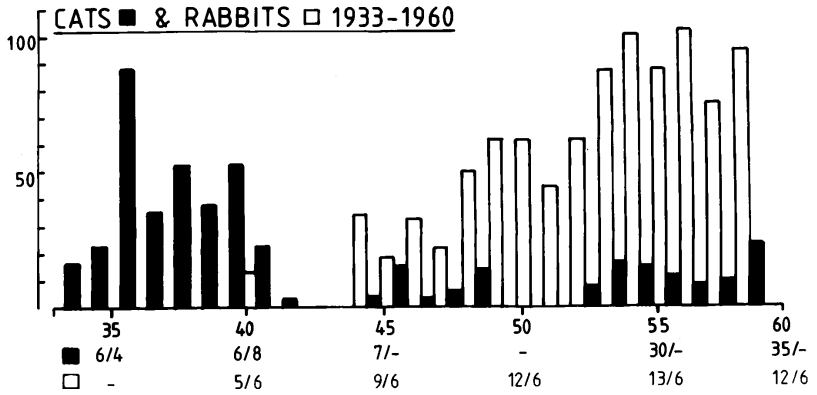

FIG. 2.
Numbers and costs of cats and rabbits used in the Department of Physiology of the University of Bristol between 1933–1960. The numbers beneath the *x*-axis give the average price per animal in shillings and pence (see Ref. 2).

MAMMALIAN PHYSIOLOGY AND THE INFLUENCE OF CHARLES SHERRINGTON

In his report on British medical education in 1912, Abraham Flexner made special mention of the decerebration techniques being developed by the neurophysiologist and later Nobel laureate Charles Sherrington, then Professor of Physiology at Liverpool. The surgery, performed under complete anesthesia, removed the pain centers in the cerebral cortex and the thalamus and effectively killed the animal, usually a small mammal such as a cat or dog. The carcass no longer required anesthesia, because it was incapable of feeling pain, and therefore did not come under the 1876 Act, which legislated for the use of animals ''capable of feeling pain,'' and could be used by students. The routine use of decerebrate preparations, often of cats, particularly by senior students became a standard feature of many British teaching laboratories.

In 1919 Sherrington, then Professor of Physiology at Oxford, published an extensive series of experiments using decerebrate and decapitate preparations. Sherrington was a strong believer in individual experience, arguing in the preface to the book that ''paradoxical though it may sound, the more skillfully a demonstration experiment is performed the less from it do some students learn,'' and so devised an extensive series of experiments that students could perform themselves on decerebrate preparations. The exercises were originally designed to be incorporated into the traditional practical courses for medical students, and in Oxford they rapidly formed an important component of the Final Honors School in physiology—an extensive and unique series of exercises on integrated mammalian physiology that was widely imitated around the world. The book itself was illustrated with experimental traces and results obtained by his students performing the exercises. Sherrington's course was approved of by no less an authority than the Government's Board of Education; as Sir George Newman, the Board's chairman, noted in 1918 the course was ''an illustration of the kind of Applied Physiology which should in my view be taught in all schools of physiology'' (23).

The legal position of these decerebrate preparations had been considered by the second Royal Commission on Animal Experimentation, which reported in 1912. They recommended that such procedures be regarded as methods of killing and therefore outside the law, although the actual technique of decerebration was clearly a procedure that should be performed under complete anesthesia by a licensee. The numbers of animals used in this manner are impossible to determine because they do not appear in official records, although the Littlewood Committee in 1963 ''formed the impression'' that large numbers were used in this way. Representations to that Committee explained that decerebrate preparations were less durable and required more experience in their use than anesthetized animals and asked for senior students to be permitted to work on fatally anesthetized animals. The Littlewood Committee viewed this proposal with some favor and recommended that the practice of allowing individual senior students to be licensed and under strict supervision controls should be continued and that decerebration of warm-blooded animals should no longer be authorized by the Act.

CATS AND ALSO RABBITS: THE BRISTOL DATA

Some indication of the numbers of small decerebrate mammals used in one department, and the prices paid, can be gained from a study of an unusual historical source, an incomplete collection of order books, ledgers, and invoices from the years 1910–1968, from the Department of Physiology of the University of Bristol (2). A number of features have enabled animal usage for class purposes to be distinguished, at various periods, from animals ordered for individual researchers; these include the use of distinguishing names and cost codes and the regularity of orders, i.e., four cats per week during term time. The order books also record the occasional order for a single cat or dog not assigned to a staff member; these appear to be for a large-scale class demonstration for a specific experimental procedure (members of staff in the department did hold the requisite C certificates), and dogs seem not to have been routinely used for class work by students. Figure 2 shows the numbers of cats and rabbits used between 1934 and 1960, expressed in academic years (from October to September), and the numbers underneath represent the average cost per animal every five years. During the late 1930s and early 1940s there is a quite marked use of cats, and there are also orders for the purchase of Sherrington decerebrators, the first as early as 1916. During much of the early period shown in this figure, the students at

Bristol were predominantly medical students—about 20–30 per year.

From the 1930s and 1940s onwards there was a steady increase in the cost of cats, which were usually obtained from farms or very occasionally from dealers. Immediately postwar, when all laboratory animals were in very short supply, it was not unusual for the department to pay 17/- (in old British currency, 12 pennies = 1 shilling and 20 shillings = 1 pound) or more for a cat, and the use of cats sharply declined. Concurrently the use of rabbits increased, and again the orders make it clear that these are also for teaching purposes—to a large extent, they probably replaced cats in the integrated mammalian practicals. Their comparative cheapness must have been a pertinent issue as class sizes continued to rise during the 1950s and 1960s (see Table 1).

ISOLATED ORGANS: FROGS

Isolated material for teaching purposes has most frequently been obtained from freshly killed frogs. Frogs have been used extensively in practical physiology—some of the earliest modern textbooks in English, for example, including John Hughes Bennett's 1872 *Textbook* and the *Handbook for the Physiological Laboratory* of 1873, depended heavily on the frog; recognized as a cheap, convenient, easily manipulated animal, its nerves, muscles, and heart could be quickly isolated, which made it ideal for several categories of experiments. Frog work in the junior physiology course usually consisted of routine experiments on nerve-muscle preparations to demonstrate contraction, fatigue, tetanus, etc. and recordings of the heartbeat with experiments on inhibition and stimulation. An extensive, but unsystematic, examination of extant practical schedules from a number of British laboratories has shown that they all contain experiments of this kind throughout the period from 1876 to 1986. Less readily available are students' notebooks, but a particularly striking early example is provided by the lecture and laboratory notebooks of W. D. Halliburton, later a well-known experimentalist and physiological writer, who for over 35 years was the author of one of the best selling physiological texts in Britain, the *Handbook of Physiology*, originally started by William Kirkes in 1848 but from 1900 officially known as *Halliburton's Handbook of Physiology* (10). As a student of John Burdon Sanderson at University College London, Halliburton completed a session of ''Physiology Proper'' in 1878–1879, also studying histology with Edward Schäfer during the same period, and his notebooks record several practical classes using frogs: nerve-muscle preparations and isolated intestine and cardiac experiments (11). In contrast with the more holistic approach taken by Sherrington, little explicit effort seems to have been made to integrate these kinds of in vitro experiments into a functional consideration of the whole animal body, although this deficit may have been remedied during lectures.

Frogs, although vertebrates, and thus protected by the 1876 Act if used in experiments calculated to give pain, were routinely decapitated or pithed before being used for teaching purposes and thus did not come under the Act and do not appear in the relevant Government statistics. This clearly poses a problem in trying to assess the level of their usage, and the order books from the Department of Physiology of the University of Bristol again provide valuable pointers, for a limited period, of the numbers of frogs used and their cost (2). These books also record the regular purchase of equipment for teaching classes—such as heart levers, moist chambers, kymographs, and frog boards. Figure 3 shows the numbers of frogs, in dozens, used between 1910 and 1960—the gaps in the histogram occur when the records are clearly incomplete because of missing volumes or pages from the existing order books. The average price per dozen is shown every five years, the prices range from one shilling and sixpence (1910) to nineteen shillings (1960). The increasing numbers used mirror quite accurately the increases in numbers of medical students throughout the 50-year period (see also Table 1), whereas the dip in numbers during the early 1940s indicates not only a reduction in student numbers because of wartime contingencies but also supply difficulties, because the order books for the period contain several orders that could not be fulfilled. From the very beginning of the analysis period, a number of different suppliers were used; local companies were sometimes supplemented by orders to companies in Birmingham and even London. Similarly, the variations during the early 1950s reflect supply difficulties, problems that are also indicated by the rise in the average cost. When it was difficult to obtain frogs, orders were often split between four or five different

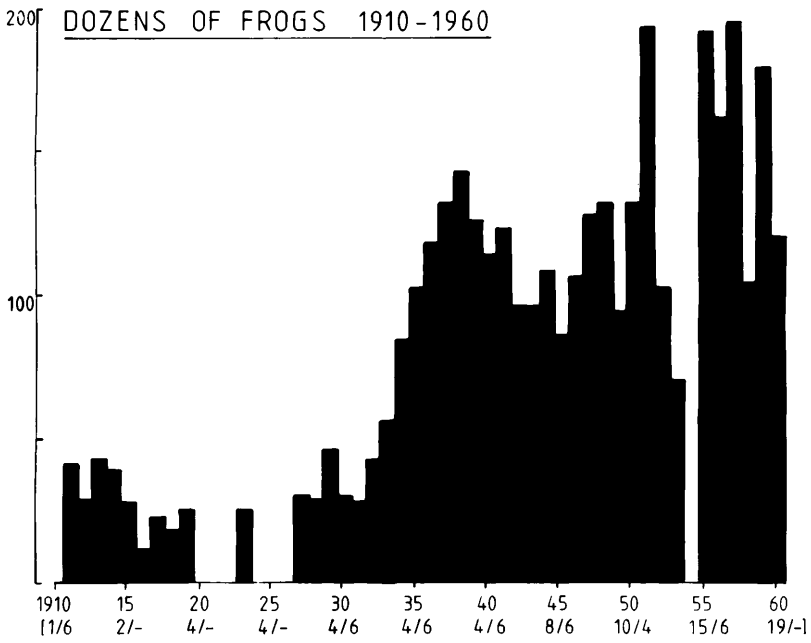

FIG. 3.

Numbers and costs of frogs used in the Department of Physiology of the University of Bristol between 1910–1960. The *y*-axis shows the numbers of frogs, in dozens, delivered to the Department, i.e., 100 represents 100 dozen, 1,200 frogs. The *x*-axis divides the period into academic years, i.e., October-September, and the numbers beneath give the average price paid for a dozen frogs in shillings and pence (see Ref. 2).

suppliers, always commercial dealers, and after the opening of the new Veterinary School in 1949–50, the department placed regular orders for its frogs with a Belgian company. The increasing use of frogs in practical physiology classes is also correlated with the implementation of curricular changes, such as those recommended by the Goodenough Committee (reported 1944) and the British Medical Association (reported 1948), as detailed below.

PHYSIOLOGY TEACHING: TIME AND NOTIONS

In 1942 in the midst of the Second World War, but with a confident eye to postwar reconstruction, the Government appointed a Committee ''to enquire into the organization of Medical Schools'' (17). The Committee, known as the Goodenough Committee after its Chairman, Sir William Goodenough, invited opinions from a wide range of individuals, institutions, societies, and other bodies, and many submitted evidence about teaching practices and requirements. Although the principal focus was on clinical teaching and its provisions, preclinical education was also considered.

The Education Subcommittee of the Physiological Society decided to use the opportunity to gather nationwide data on how physiology was taught. Surveys were sent to each of 26 departments, asking for information on staffing levels and student numbers and for a detailed breakdown of hours spent teaching different components of the course. Figure 4 summarizes the information provided by 23 departments (no reply was received from Cardiff or King's College London, and the Royal ''Dick'' Veterinary School of Edinburgh taught only veterinary students) on the teaching of physiology to medical students, although some departments reported that their figures also included specialized teaching to science students. Additional data reported on the teaching of dental and veterinary students have not been included.

The range of practical work provided, either completely or in collaboration with another department, closely resembles that described to the Royal Commission in 1875, that is, physiology still comprised three distinct components, histology, chemical physiology

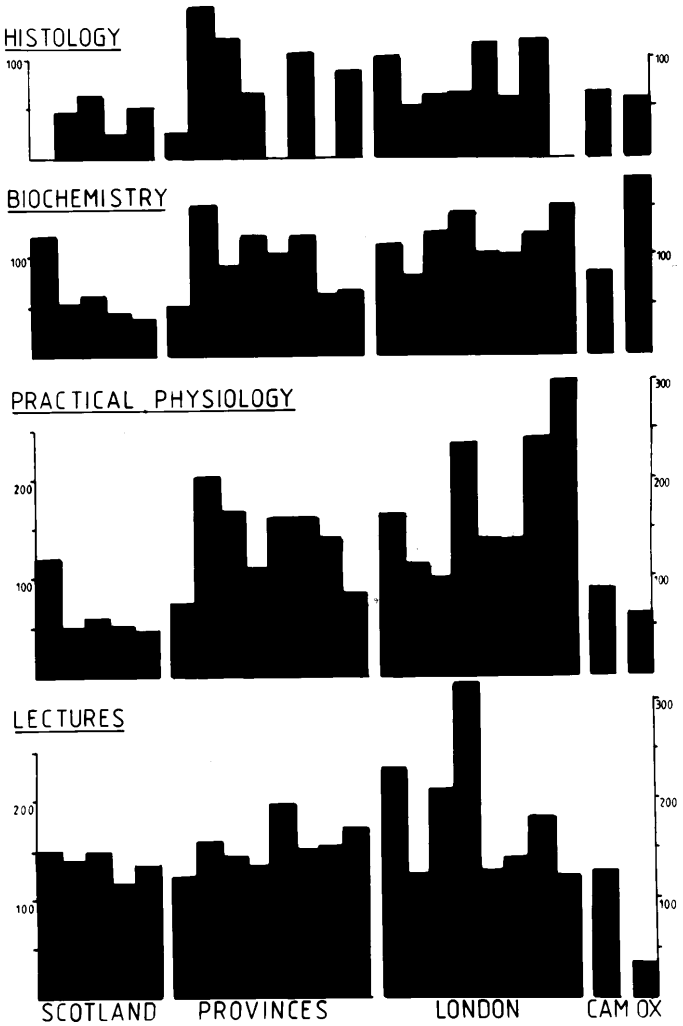

FIG. 4.

Hours spent in each of 23 departments of physiology in teaching different aspects of the subject, by lectures or practical classes in histology, biochemistry, or practical physiology (see Ref. 18). The Scottish Universities are, from *left* **to** *right*, **Aberdeen, Dundee (St. Andrews), St. Andrews, Edinburgh, Glasgow. Provincial Universities are,** *left* **to** *right*, **Belfast, Birmingham, Bristol, Durham (Newcastle), Leeds, Liverpool, Manchester, Sheffield. London Medical Schools are,** *left* **to** *right*, **St. Bartholomew's, Guy's, London, Middlesex, Royal Free, St. Mary's, St. Thomas', University College. The final entries are from Cambridge and Oxford.**

or biochemistry, and practical or experimental physiology, which were all taught in the same department. Four departments (Aberdeen, Leeds, Manchester, University College London) no longer taught histology, that responsibility having passed to the anatomy department (although, interestingly, the physiology department in Aberdeen later reclaimed histology teaching). All departments still taught biochemistry, the new name for chemical physiology, either from within the normal staff complement of the department or from a formal subdepartment, many of these later becoming independent departments of biochem-

istry. All the physiology departments also taught practical, or experimental, physiology, and it is these two latter courses that required experimental animals to be used, either in vivo or in vitro. As Fig. 4 clearly illustrates, there was considerable variation in the hours devoted to the subject. Of the Scottish Universities surveyed only Aberdeen taught more than 100 hours per year of practical physiology classes, whereas several of the English schools taught more than 150 hours per year, University College London easily topping the league with 300 hours of laboratory teaching in experimental physiology alone (18).

The summarized data from this survey were presented by the Physiological Society in their written evidence to the Goodenough Committee, but the Committee's main concerns were on consolidating the diverse components of the medical course into a seamless educational experience, arguing that ''a better educational approach would be provided by a closer integration of the teaching in anatomy, physiology, biochemistry and pharmacology.'' They clearly expressed a forceful proposition that physiology should be better integrated with clinical work and that human subjects, including patients, could and should be used in practical work. They made a formal recommendation that there should be, in the preclinical courses, ''a drastic elimination from their teaching and the examinations of a mass of detailed information.'' Although not specifically directed at physiologists, the comment clearly includes the mass of physiological teaching being presented to medical students. One immediate respondent to this call was the eminent physiologist and cardiologist Sir Thomas Lewis, who compiled a set of physiological exercises to be performed on the human subject (14). These were ''road-tested'' by the undergraduate students of University College London, then evacuated from central London and living and working in Leatherhead, Surrey. The response from the students and their teachers was enormously favorable, the Dean of the Medical School writing to Lewis, ''We all of us feel, with no little enthusiasm, that we should like your manuscript published just as it stands. It promises to have an influence on the teaching of physiology, comparable to that of Sherrington's *Mammalian Physiology*, and it would be a pity to dilute its message by adding to it experiments on other lines.... I feel confident that physiologists would welcome the book, and though, as in the case of Sherrington's book, its influence would not come to full fruition for many years ... the influence would be in the direction with which physiologists would have great sympathy'' (15).

Medical education came under further review almost immediately after the Second World War when, in 1945, the British Medical Association appointed a Medical Curriculum Committee to examine what they considered to be the most appropriate training necessary for a doctor. They reported in 1948, a year of tremendous change for British medicine as the National Health Service came into being that year, and they too highlighted the difficulties that the Goodenough Committee had recognized, of the overcrowding of the medical curriculum and the unnecessary experimental work that some medical students were expected to complete. Their report uses blunter language than had the Goodenough Committee: ''A major criticism of the course in physiology is that an excessive amount of time and effort appears to be devoted in some schools to animal experimental physiology.'' The Committee elaborated their concerns, recognizing ''that the student... tends to overestimate the importance of technical skill and fails to appreciate that the true purpose of animal experimental physiology is to help him to acquire knowledge which cannot be gained by observation and experiment on human subjects, and to illustrate physiological reactions and properties which cannot otherwise be demonstrated.'' They recommended a core series of experiments that they believed possessed genuine educational value for general medical students, as opposed to senior students specializing in physiology. These included: experiments on frog muscle-nerve preparations to illustrate some of the important properties of these tissues; experiments with the frog heart to show the properties of cardiac muscle: the effect of cardiac nerves on the heart, the mode of conduction of the beat, heart block, and the effect of temperature and of ions on the beat; perfusion experiments on frog blood vessels, to show the action of drugs such as adrenaline; and experiments with rabbit organs on the perfused mammalian heart and on isolated intestines (3). Extrapolating from the Bristol University data (Fig. 3), a marked increase in the use of frogs in practical physiology teaching is indicated, which is undoubtedly a consequence of the recommendations

of the Goodenough Committee and the British Medical Association.

By 1975, when the General Medical Council undertook a further survey of medical education, 34 departments of physiology were assessed. Most departments were, by then, providing basic laboratory classes using the simple in vitro preparations recommended by the British Medical Association's Committee. Several schools had also developed practical classes that depended heavily on medical students using each other as experimental animals and also attending clinical demonstrations on patients, to illuminate physiological principles. Many departments also reported the regular use of tape-slide programs, videos, and films (8). These developments coincided with the prominent drop in Certificate C returns already noted (Fig. 1).

ANIMALS OUTSIDE THE 1876 ACT

As already noted, not all animals used for teaching purposes, either in physiology or in cognate sciences, were used in experiments performed under the authority of Certificate C of the 1876 Act. Animals killed for the removal of organs, etc. and decerebrate preparations were not covered by the Law, and therefore their numbers are not recorded in the official statistics and reports used above. One unusual source of information about the total numbers of animals used comes from a survey undertaken in 1953 by the MRC's Laboratory Animals Bureau of requirements for animals in the previous year. This Bureau was established by the MRC immediately after the Second World War, in 1947, with the principal aim of breeding and providing guaranteed supplies of experimental animals to MRC Research Units and MRC-supported scientists around the country. Teaching needs of universities and medical schools had also been taken into consideration, although satisfying such requirements was not a prime consideration of the Bureau. In addition to MRC research establishments, university, medical school, hospital, and commercial laboratories were all questioned about their usage of animals, and one category used in the subsequent analysis was ''teaching,'' for which 34,337 animals were used during 1952 (see Table 3). Unfortunately, the report announced, somewhat inaccurately, ''teaching is self-explanatory,'' and so included no further details of the uses to which these animals were put. In that year, C certificate returns were approximately 2,500 (see Fig. 1), and so these data, which do of course include all biological and medical teaching, emphasize that there was a large amount of animal usage outside the restriction of the Act.

TABLE 3
Types of laboratory animals used for teaching in 1952 (Ref. 16)

Guinea pigs	9,388	Horses	17
Hamsters	10	Pigs	0
Mice	11,243	Sheep	0
Rabbits	730	Primates	3
Rats	6,867	Other mammals	3
Cats	609	Canaries	0
Dogs	157	Chickens	368
Ferrets	4	Pigeons	230
Cows	3	Reptiles	52
Goats	19	Amphibia	4,634
		TOTAL	34,337

The Bureau also sought information about the source of these animals, and Table 4 indicates that the vast majority of guinea pigs, rabbits, and chickens were bought in from specialized breeders or animal dealers. Rats and mice, both used in large numbers, were also frequently obtained from colonies maintained in the respondents' own or other, noncommercial laboratories.

TOWARD THE 1986 ANIMALS (SCIENTIFIC PROCEDURES) ACT

The publication in 1973 of Richard Ryder's *Victims of Science* opened up fresh debates about the use of experimental animals and fueled renewed, organized, and even terrorist activity from and on behalf of antivivisectionist groups. Ryder made little direct mention of the use of animals in teaching, confining his remarks to classroom dissections in schools and commenting adversely on the Home Office practice of

TABLE 4
Sources of animals used for teaching during 1952 (Ref. 16)

	Breeder	Dealer	Other	Own Lab
Mice	8,080	263	200	2,700
Guinea pigs	873	7,509	117	889
Rabbits	12	675	0	42
Rats	0	2,330	48	4,489
Chickens	0	368	0	0

licensing senior undergraduates (21). In 1977 there was a marked change in the way the annual Home Office statistics were presented to Parliament, and this new approach can be seen as a response to antivivisectionist concerns about which types of animals were used in what kinds of experiments. Somewhat confusing the original conditions of Certificates C and D, the Chief Inspector reported ''special provision for the *demonstration of known facts* is dealt with under a certificate C'' (my emphasis) and proceeded to provide an extremely detailed breakdown of the numbers of animals used in teaching. A total of 2,736 experiments were reported under Certificate C in 1977, and Table 5 shows the types of animals reported to the Home Office in that year, revealing that the predominant number of animals on which experiments were demonstrated were rodents (1,937 in total).

With clear sensitivity to criticisms of the use of animals in demonstrations, the Inspector further analyzed the returns, classifying the type of experiment for which the animals were used, as shown in Table 6. Perhaps unfortunately, the classification system offered to licensees was such that the vast majority of experiments could not be classified, which some critics found disturbing rather than reassuring.

The Home Office undertook yet a further analysis, again stimulated by criticisms that cruel techniques were demonstrated to students, by recording the methods used in demonstrations (see Table 7). The types of specific questions asked indicate the areas where concern was being raised, i.e., experimental interference with the central nervous system or special senses, the deliberate infliction of a potentially painful injury. However, the limited classifications offered to licensees again meant that the vast majority of experiments were unclassified, which brought further criticism.

TABLE 5
Types of animals reported under Certificate C in 1977

Mouse	486	Cat	270
Rat	1,326	Dog	40
Guinea pig	113	Horse, donkey	0
Other rodents	12	Bird	35
Rabbits	404	Fish	12
Primate	0	Other	38
		TOTAL	2,736

TABLE 6
Types of experiments for which the animals in Table 5 were used

Acute toxicity	200
Chronic toxicity	0
Teratogenicity	2
Distribution, metabolism of substances	153
More than one of the above	60
Others	2,321
TOTAL	2,736

Widespread agitation by antivivisectionists, animal welfare groups, and others led to the increasing acceptance by the Government and the scientific community that the 1876 Cruelty to Animals Act had to be replaced. That replacement legislation, the Animals (Scientific Procedures) Act of 1986, authorized animal experimenters by means of a personal license and an additional project license that defined categories of purpose, one of which is ''education or training otherwise than in primary or secondary schools.'' Thus it is still possible, under current legislation, to use animals in the teaching of practical physiology.

The history of the use of animals in teaching physiology in Britain during the past 130 years closely reflects the history of British physiology as a whole. Although the imposition of restrictions in 1876 was initially met by hostility, these were gradually used to advantage,

TABLE 7
Experiments returned under Certificate C in 1977, classified by technique used

Interference with special senses or brain centers controllng		Infliction of physical trauma to simulate human injury (not burning or scalding)	12
a) Behavioral purposes	0	Inhalation	21
b) Other purposes	9		
Interference with CNS (other than centers controlling special senses)		Application of substance to eye	0
a) Behavioral	224		
b) Other	114	More than one of the above	69
Use of aversive stimuli		Others	2,287
a) Behavioral training	0		
b) To induce psychological stress	0		
		TOTAL	2,736

creating well-managed conditions under which physiology prospered, as evidenced by Abraham Flexner's report of 1912. Additionally, the development of alternative approaches, such as using decerebrate and in vitro preparations, allowed for wide-scale experience of practical physiology by all students, especially medical students. It was not until after the Second World War, when medical education was reassessed, that this emphasis was called into question and practical courses for medical students were radically restructured to include fewer, if any, whole animal experiments or demonstrations. Senior students majoring in physiology continued, and continue, to use such procedures in their specialized training, although increasingly alternative teaching techniques were introduced into their curricula.

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