

MAMMALIAN PHYSIOLOGY

LIDDELL & SHERRINGTON

MAMMALIAN PHYSIOLOGY

A COURSE OF PRACTICAL EXERCISES

A NEW EDITION

BY

E. G. T. LIDDELL

D.M., FELLOW OF TRINITY COLLEGE
OXFORD

AND

SIR CHARLES SHERRINGTON, O.M.

M.D., D.Sc. (CANTAB.), F.R.S.

WAYNFLETE PROFESSOR OF PHYSIOLOGY IN THE
UNIVERSITY OF OXFORD

OXFORD

AT THE CLARENDON PRESS
LONDON : HUMPHREY MILFORD

1929

Printed in Great Britain

TO
OUR CLASS PUPILS

PREFACE TO SECOND EDITION

IN the preparation of this new edition I have invited the collaboration of my friend and colleague Dr. E. G. T. Liddell of Trinity College. He and I have been associated already through a number of years in teaching from the book. He has undertaken much of the labour of the revision. That his experience should thus be utilized and his judgement made of service here is at once a pleasure to me and an advantage to the reader.

C. S. S.

THE exhaustion of the original edition has given opportunity to revise this book for reissue. Some rearrangement of the exercises has been made and new matter has been introduced. One new exercise has been added. Our intention has been to bring the practical work up to date in scope and method, according as experience has directed.

It is a pleasure to tender here our grateful acknowledgements to friends and colleagues, some at hand, some at a distance, for kindly advice and suggestions. In particular we are indebted to Professor J. Mellanby, F.R.S., for Exercise XXI, to Dr. Howard Florey in respect of Exercise XXII, and to Miss S. Cooper and Mr. R. S. Creed for the observation with the oncometer, as well as for their help in many other ways.

E. G. T. L.

C. S. S.

OXFORD.

September, 1929.

PREFACE TO FIRST EDITION

A CERTAIN broadening of scope of the practical work customary among us for students in animal physiology has become desirable, and has seemed so for some time past in the opinion of not a few. A number of facts fundamental to physiology can be seen by the student very readily and appropriately in the frog. But other facts there are, of great value and interest especially to the future practitioner of medicine, which can be better displayed and more easily obtained in the mammalian preparation. Although that preparation as available for a class-student is merely a carcase, the circulatory activity which it retains for the time being, and the temporary survival of many of its glandular and muscular tissues and of its simpler nervous structures, render obtainable from it under suitable precautions a number of reactions which can be studied with extreme advantage by the student for himself. The exercises detailed in the following pages consist of experiments of that kind. Several of them are repetitions, simplified in accordance with the limits of the preparation and of the student's experience, of famous observations which in the hands of the masters who first made them marked distinct advances in natural knowledge. The particular experiments chosen are of course not the only ones which might have been selected. In such a choice each teacher will to some extent have his own predilections. The mammalian preparation decapitate or decerebrate is capable of serving many uses for practical class-instruction. The particular experiments included here are, however, all such as experience actually proves the student to be well able, with ordinary care on his part and some supervision on the part of his teacher, to accomplish successfully for himself. The actual performance by the student of some few such main experiments gives him, I am convinced, a better insight into their general significance and into the problems they touch than does any mere inspection at a demonstration however skilfully conducted. Indeed, paradoxical though it may sound, the more skilfully a demonstration experiment is performed the less from it do some students learn.

The course as arranged here has taken shape gradually under experience during the endeavour to devise the kind of teaching needed. It has come to comprise twenty-two lessons, each consisting of somewhat less than three hours' work. On the twenty-four lesson cycle as followed in this University,

two class-meetings remain over for repetition of such particular items as the student may want to revise before examination.

To the student's directions for each exercise is subjoined a short annotation concerning the source and bearings of some of the more salient observations included in the exercise. If in these remarks the trend is often historical, it is because that approach has seemed to enable the student best to assess for himself the intellectual cost and value of the observations he is repeating.

The illustrations supplied both in the plates and text-figures have all been drawn from preparations and apparatus as used in the class. The graphic records reproduced have been obtained by the class-students themselves. At the end of the volume an Appendix contains suggestions as to methods of arrangement and preparation for the class based on experience of its actual working.

The interest uniformly shown by the class-students has furnished evidence welcome to me that the course in their eyes possesses real utility. In many instances a fresh impulse seemed to have been imparted to their physiological study. The class-work has certainly vivified for them the reading of the systematic texts.

I am not so sanguine as to suppose that the choice of method or the selection of object which I have adopted will always appeal to others as the best. Nor can I hope to have escaped, in a venture like the present, all errors of omission or commission. I would, however, say that I have been at pains throughout to choose the suitable and to describe it correctly. As it is, the course and its syllabus have been cited with approval in a Memorandum issued by the Board of Education last year. Sir George Newman states that the course is there drawn attention to 'as an illustration of the kind of Applied Physiology which should in my view be taught in all schools of physiology'.

By some of those who have taken the course I have been told that they traced to it a measure of facility in technique which proved of service to them when entering upon independent investigation later on in one field or another of experimental medicine.

C. S. S.

MAGDALEN COLLEGE,
OXFORD, *February* 1919

LIST OF PLATES

PLATE

- I. Inspection of heart and lungs *in situ*. Exerc. IV.
- II. Preparation of carotid and vagus. Arrangement of Hg manometer for arterial pressure. Exerc. V, &c. Plan of innominate and subclavian ligations for aortic valve experiment. Exerc. VIII.
- III. Splanchnic nerve experiment. Exerc. VII.
- IV. Accelerator nerve experiment. Exerc. IX.
- V. Hydraemic plethora experiment. Exerc. X. Preparation of external jugular vein. Exerc. VI. Cervical sympathetic on the blood-vessels of the ear. Exerc. XVII.
- VI. Salivary secretion experiment. Exerc. XII. Electrode for unipolar stimulation. Exerc. V.
- VII. Magendie's experiment on the spinal nerve-roots. Exerc. XV.
- VIII. Conductive direction of spinal nerve-root tested by pinna reflex. Exerc. XVI.
- IX. Direct and reflex reactions of mammalian nerve-muscle preparation. Exerc. XVIII, XIX, XX.

CONTENTS

LIST OF PLATES xii

EXERCISES

I. Obs.	1.	Intestinal movement and tone	1
„	2.	Adrenal extract on intestinal movement and tone	2
„	3.	Adrenal extract on spleen	2
„	4.	Adrenal extract on arterial wall	5
II.	5.	Revival of beat of the excised heart by coronary perfusion	7
„	6.	Influence of temperature on beat	10
„	7.	Cooling and warming the pacemaker	10
III.	8.	Chloroform on excised mammalian heart	13
„	9.	Adrenal extract on excised mammalian heart	13
IV.	10.	Inspection of the lungs and beating heart <i>in situ</i>	17
„	11.	Effect of raising intrapericardial pressure	18
„	12.	Further inspection of heart and great vessels <i>in situ</i>	18
„	13.	Inspection of the heart inhibited by the vagus	19
„	14.	Inspection of capillary circulation	19
„	15.	Measurement of speed of flow of blood in a capillary vessel	20
V.	16.	Graphic record of carotid pressure	26
„	17.	Stimulation of distal vagus on arterial pressure	26
„	18.	Escape of ventricle from vagus, and influence of adrenal extract upon	28
„	19.	Paralysis of cardiac vagus by atropine	31
VI.	22.	Adrenal extract on arterial pressure	33
„	23.	Asphyxia and arterial pressure	33
„	24.	Amyl nitrite and arterial pressure	36
„	25.	Measurement of venous pressure	36
„	26.	Occlusion of the coronary arteries on heart-beat	37
VII.	27.	Distal end of n. splanchnicus on arterial pressure	40
„	28.	The adrenal gland and the splanchnic reaction	41
„	31.	Pituitary extract and arterial pressure	44
„	32.	Splanchnic n. vasoconstriction in kidney and gut	44
„	33 A.	Inspection of chyle and lacteals	44
„	34.	Chromaffin reaction of adrenal medulla	44
„	35.	Time of the lesser circulation	44
VIII.	37.	Aortic insufficiency on arterial pressure and pulse	50
„	38.	Reducing action of the tissues on methylene blue	51
„	37.	(Continued) Calibration of membrane manometer	54
IX.	39.	Heart rate and n. accelerantes	56
„	40.	Gravity and arterial pressure	59
„	41.	Recurrent laryngeal and the vocal cords	59
X.	42.	Renal secretion and venous injection of saline	61

X.	Obs.	43.	Diuresis by urea	63
	"	44.	Diuresis by pituitary extract	64
	"	45.	Diuresis by caffeine citrate	64
	"	46 A.	Detrusor action of n. pelvici	64
XI.	"	47.	Specific gravity of the blood	66
	"	48.	Dilution of the circulating blood by saline injection	67
	"	49.	Haemorrhage and sp. gr. of blood	68
	"	50.	Perfusion of kidney with normal saline	68
	"	51.	Adrenal extract and the renal vessels	69
	"	52.	Amyl nitrite and the renal vessels	69
XII.	"	54.	Secretory action of corda tympani	72
	"	55.	Pilocarpine and salivary secretion	73
	"	56.	Atropine and salivary secretion	73
	"	57.	Air-embolism	73
	"	58.	Expansion of the lungs by aspiration: pneumothorax	73
XIII.	"	59.	Inspection of respiratory movements of larynx	76
	"	60.	Reflex swallowing	76
	"	61.	Reflex closure of glottis: cough	77
	"	62.	Graphic of respiratory movements of chest	77
	"	63.	Phagetic efficacy of water, dilute alcohol and oil. Arrest of respiratory movement by swallowing	77
	"	64.	Reflex swallowing by stimulation of superior laryngeal nerve	78
	"	65.	Vagus and respiratory rhythm	80
XIV.	"	66.	Vasopressor reflex	81
	"	67.	Depressor nerve	82
	"	68.	Respiratory waves of the arterial pressure	83
	"	69.	Reflex cardiac inhibition	84
XV.	"	70.	The spinal knee-jerk	86
	"	71.	Conductive direction of the spinal roots	86
	"	72.	Galvani's experiment with metals	90
XVI.	"	73.	The decerebrate knee-jerk	92
	"	74.	The rule of the roots tested by pinna reflex	93
	"	75.	Head-shake reflex of auditory meatus	95
XVII.	"	77.	Cervical sympathetic and vessels of the pinna	96
	"	78.	Circulatory changes and the volume of the kidney	97
	"	79.	Haemorrhage and arterial pressure	98
	"	80.	Restoration of arterial pressure by gum-saline injection	98
	"	81.	Retardation of clotting by 'decalcification'	99
XVIII.	"	82.	Proprioceptive reflex of tibialis anticus	103
	"	83.	Reflex of ankle flexor to single break-shock	105
	"	84.	Motor twitch contraction compared with reflex	106
	"	85.	Measurement of latencies of reflex and motor twitch	107
XIX.	"	86.	The 'shortening reaction'	109

CONTENTS

xi

XIX.	Obs. 87.	The stretch-reflex	109
	„ 88.	The 'lengthening reaction'	110
	„ 89.	Reflex inhibition of posture	110
	„ 90.	Reflex inhibition of contraction	110
XX.	„ 92.	Inhibitory action of cerebellar cortex	113
	„ 93.	Spinal transection on decerebrate rigidity	116
	„ 94 A.	Spinal reflex flexor tetanus	117
	„ 94 B.	Motor-nerve tetanus	117
XXI.	„ 96.	Action of secretin	118
	„ 97.	The flow of bile after the intravenous injection of (a) secretin (b) bile salts	120
XXII.	„ 101.	Intravenous injection of bacteria	122
	„ 102.	Phagocytosis of bacteria	123
	„ 103.	Amoeboid movement of leucocytes. Phagocytosis of carmine particles	123
	„ 104.	Fate of intravenously injected bacteria	124

Observations additional to the preceding, which may be omitted at the first performance of the exercises

V.	Obs. 20.	Arterial pressure and faradization of the spinal cord	126
	„ 21.	Antidrome conduction in the spinal cord	126
VII.	„ 29.	Central end of n. splanchnicus on arterial pressure	128
	„ 30.	Asphyxia on arterial pressure after section of both n. splanchnici	128
	„ 33 B.	Lymphatic drainage of peritoneal cavity through the diaphragm	128
VIII.	„ 36.	Aortic stenosis on arterial pressure and pulse	129
X.	„ 46 B.	Reflex contraction of the bladder	129
XII.	„ 53.	Reflex salivary secretion	129
XVI.	„ 76.	The rule of the roots and the pinna reflex	130
XIX.	„ 91.	Reflex rhythm in crossed extensor reflex	131
XX.	„ 95.	Occlusion of reflex effect	131
XXI.	„ 98.	The flow of pancreatic juice and bile after injecting bile into the duodenum	132
	„ 99.	The flow of bile only after injecting bile into the ileum	132
	„ 100.	Absorption of fat into the lacteals of the small intestine	133
APPENDIX			135
INDEX OF NAMES			161

EXERCISE I

RHYTHMIC MOVEMENT AND TONE OF INTESTINE; INFLUENCE OF ADRENAL EXTRACT ON INTESTINE, SPLEEN, AND ARTERIAL WALL

I. SEE that your recording apparatus is in order, and that the recording surface travels from right to left about 15 mm. a minute. Attach a rubber or glass syringe to the rubber tube at end of the glass tube (G, text-fig. 1) on standard and blow some air through the Ringer-Locke solution in the beaker.

II. *Dissection.* In the carcase of the freshly-killed rabbit, provided for you in the tray, open the abdomen freely in the mid-line and excise with scissors about 10 cm. length of small intestine, emptying it by gentle pressure with the fingers before excising it. The duodenum usually affords a better preparation than the ileum; but the piece should not be taken from quite close to pylorus. Place it in cold Ringer-Locke fluid. Also the spleen; also a piece of the thoracic aorta about 5 cm. long. Take care in excising these to handle them with as little damage to them as possible.

III. From the length of small intestine lying in the cold 'Ringer-Locke' cut off with sharp scissors by two clean cuts a piece 2 cm. long. It will measure longer when it is relaxed. Holding this gently with the fingers, pass through its wall about 3 mm. from the cut edge a needle carrying a thread. Withdraw needle and by the thread tie the gut closely down to the taper bent end of the glass tube affixed to the table-standard. Attach a pin-hook and thread through the lip of the opposite end of the intestine.

OBS. 1.
Intestinal move-
ment and tone.

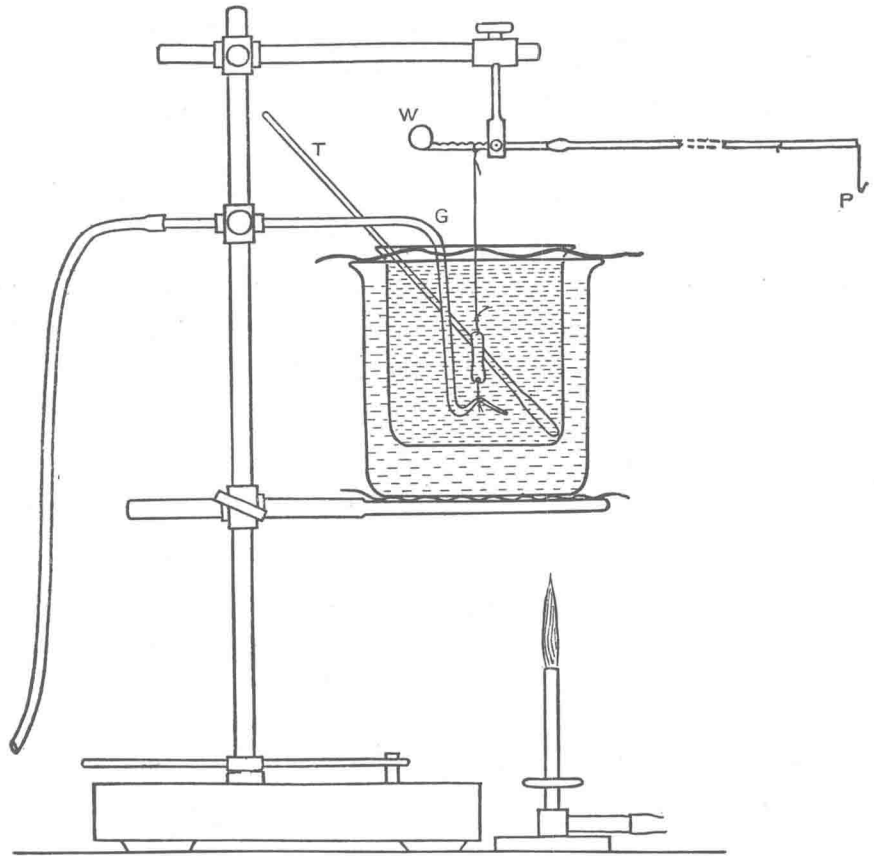
Place the piece of intestine thus attached to the glass tube in the beaker of cold Ringer-Locke fluid so that intestine is wholly plunged; clamp glass tube in position on the vertical standard. Bring the shorter arm of the writing lever vertically over intestine; slip over it a non-slip loop of the thread from intestine. Nearly counterpoise lever (with a small lump of clay, W, text-fig. 1) so as to allow 'tonus' as well as 'beat' of intestine to show.

See that the glass style (P, text-fig. 1) at end of lever's long arm—which may have with advantage a length of 30 cm.—marks at all heights on drum surface and over a considerable arc. Place a small low gas-flame under the outside beaker which serves for water-bath to the inner beaker.

Start the recording drum; note movements of intestine, beginning when thermometer in inner beaker indicates about 30° C. Later, when bath is at 35° C., withdraw the gas-flame. The beats will be about 10–20 a minute.

OBS. 2.
Adrenal extract
on intestinal
movement and
tone.

IV. Add 0.5 c.c. of solution of adrenalin (i.e. adrenal extract) 0.01 per cent. to the Ringer-Locke fluid (about 300 c.c.) in the beaker. Note the effect (1) on the beat and (2) on the tonic length of the strip. Note the slight pink



TEXT-FIG. 1. Arrangement for recording movements of intestinal strip in warmed Ringer-Locke fluid. G, tube for aerating the fluid and serving as fixation for thread from intestinal strip; P, glass writing-point slung in sleeve end of straw lever; W, counterpoise for writing lever; T, thermometer. The vertical standard carrying both water-bath and recording lever rotates in its base up to the small stop on the base, allowing adjustment to the recording surface by a single movement.

colour gradually tinging the solution. [Try the ileocolic sphincter's contraction with adrenalin.]

OBS. 3.
Adrenal extract
on spleen.

V. Empty and rinse out the inner beaker. Refill it with cold Ringer-Locke fluid and blow some air through as before. Fix a strip of excised spleen to glass tube in the bath and to writing lever above, lengthwise

EXERCISE VI

ARTERIAL-PRESSURE RECORD; INFLUENCE OF ADRENAL EXTRACT; OF ASPHYXIA; AND OF AMYL NITRITE; MEASUREMENT OF VENOUS PRESSURE; OCCLUSION OF CORONARY VESSELS

I. A decapitated carcase supplied with pulmonary ventilation is provided as for exerc. IV. See as in exerc. IV that it is in good order.

II. Set the Ringer-Locke fluid warming and get ready the instruments and apparatus for a kymographic record, and for intravenous injection by the needle-syringe. Get ready also a manometer for observation of venous pressure. This latter manometer contains half-saturated Na_2SO_4 solution instead of Hg, has no float, its junctional tubing is not pressure-tubing, and it has no reservoir-bottle attached to it; no graphic record is taken by it, so that it need not be brought up to the kymograph, but it should have a paper scale in cm. marked on its mounting for reading the venous pressures by. Have ready glass cannula for insertion into vein. See that you have also at hand (1) adrenal extract, (2) amyl nitrite, (3) a few fine entomological pins.

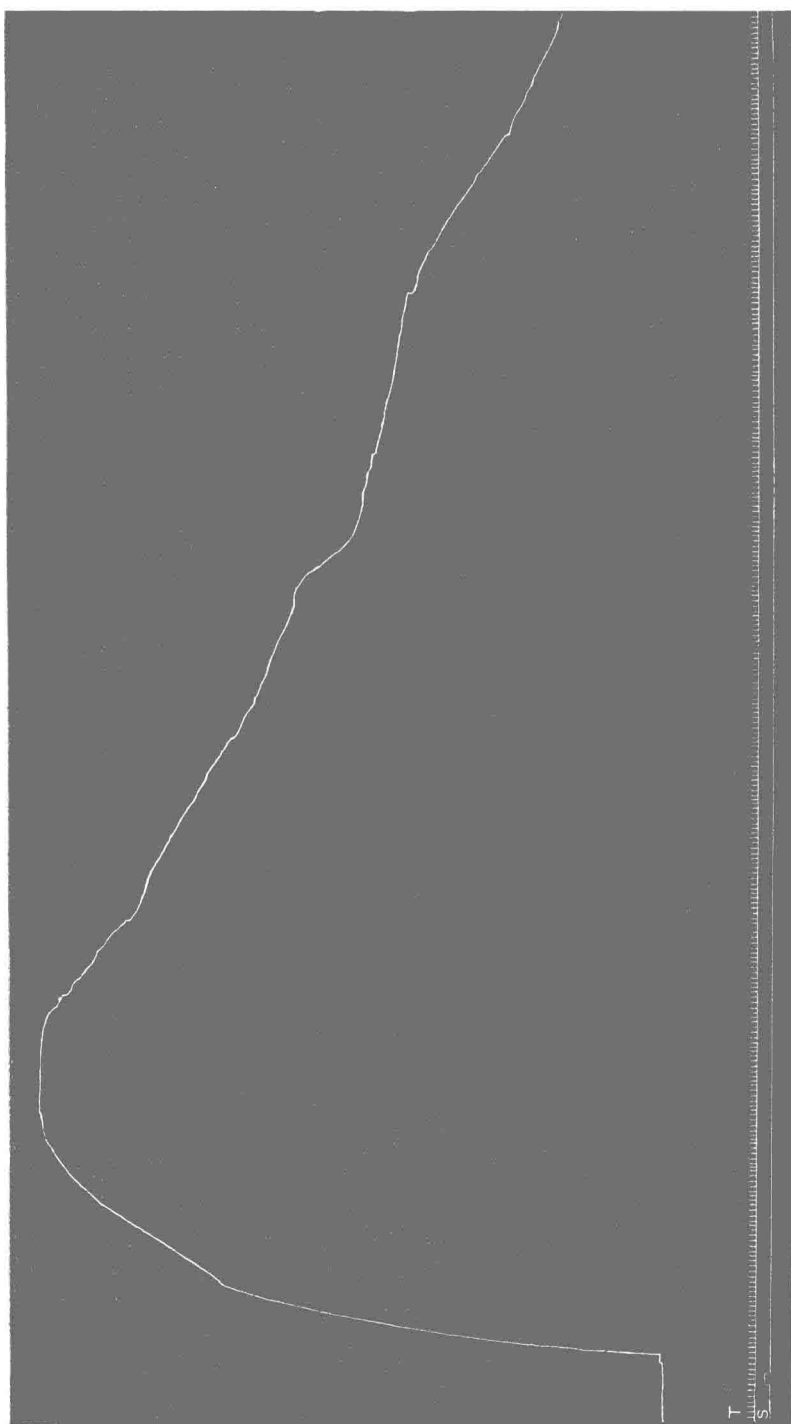
III. *Operation.* Expose one of the carotids (see exerc. V), preferably left, leaving right side free for external jugular vein later; attach to the artery the Hg manometer, &c., as in last exercise, and obtain an arterial-pressure record by the kymograph as last time.

IV. Give an injection of adrenal extract by the great saphenous vein (see exerc. V). The dose may be $\frac{1}{2}$ c.c. of the 0.1 per cent. solution of adrenalin provided for you. It should be injected while the kymograph is running (text-fig. 17). Note the resulting rise of arterial pressure.

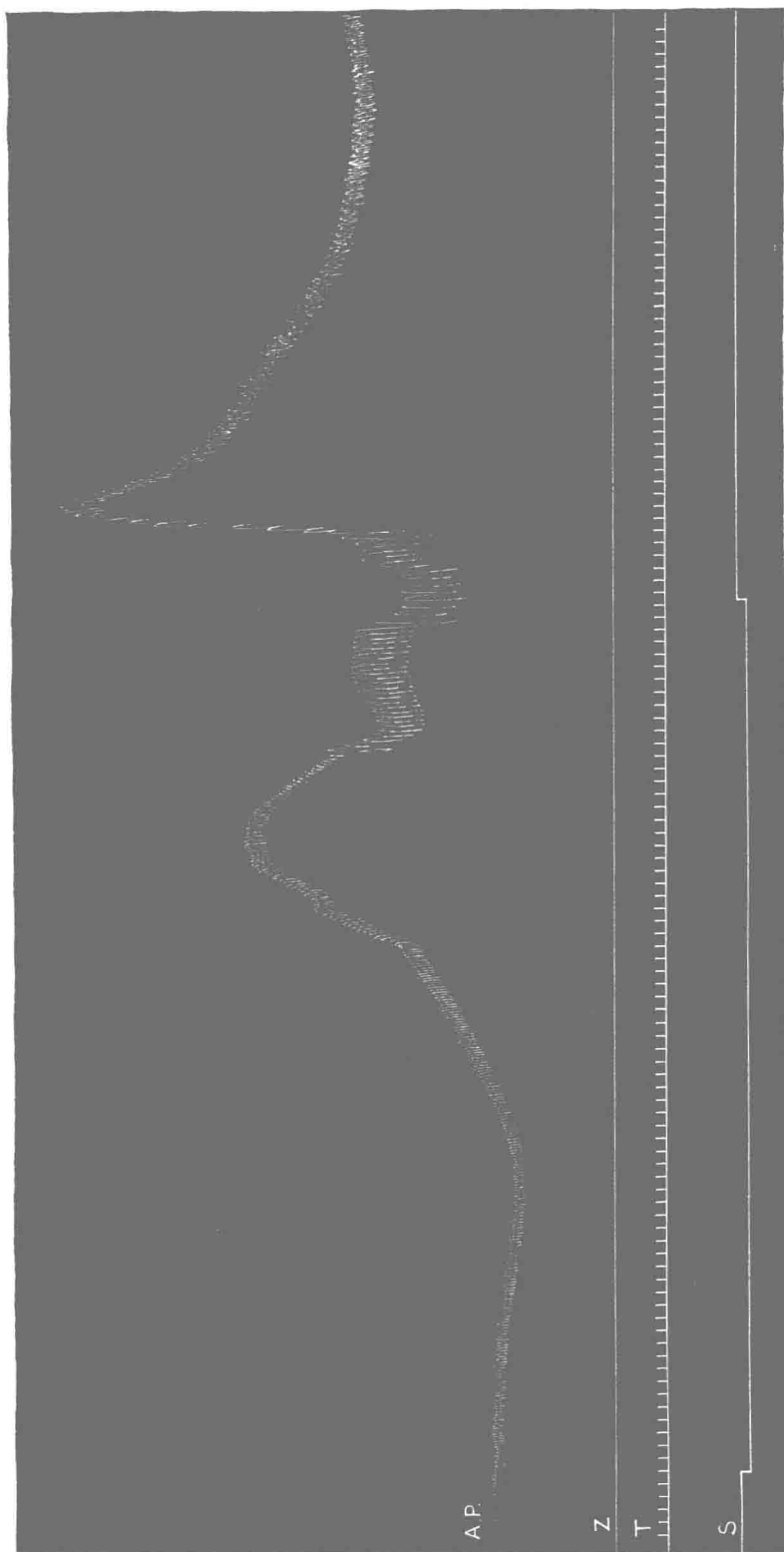
OBS. 22.
Adrenal extract
on arterial
pressure.

V. Set the kymograph running, and after half a minute or so clamp or detach the rubber tube from the respiration-pump to the trachea. Note the resulting disappearance of respiratory undulations from the arterial-pressure record. Observe the colour of the blood in the arterial cannula; its bright arterial tint will continue for many seconds, and the pressure record will show little further change so long as the scarlet colour in the cannula continues. After a variable but always lengthy period, e.g. 100–200 secs., the blood will rather suddenly darken, and then a rise of a. p. will take place. Following this there usually occurs (text-fig. 18) a change in the rate of the heart-beat, the rate falling suddenly to one-half, and then

OBS. 23.
Asphyxia and
arterial pressure.



TEXT-FIG. 3. Strip of excised spleen (rabbit) in Ringer-Locke fluid at 35° C.; contraction caused by adrenal extract (J. M. Smith).
T, time in 2" intervals; S, signal indicating when adrenal extract was added to the fluid, giving a dilution of 1 in 5,000,000.

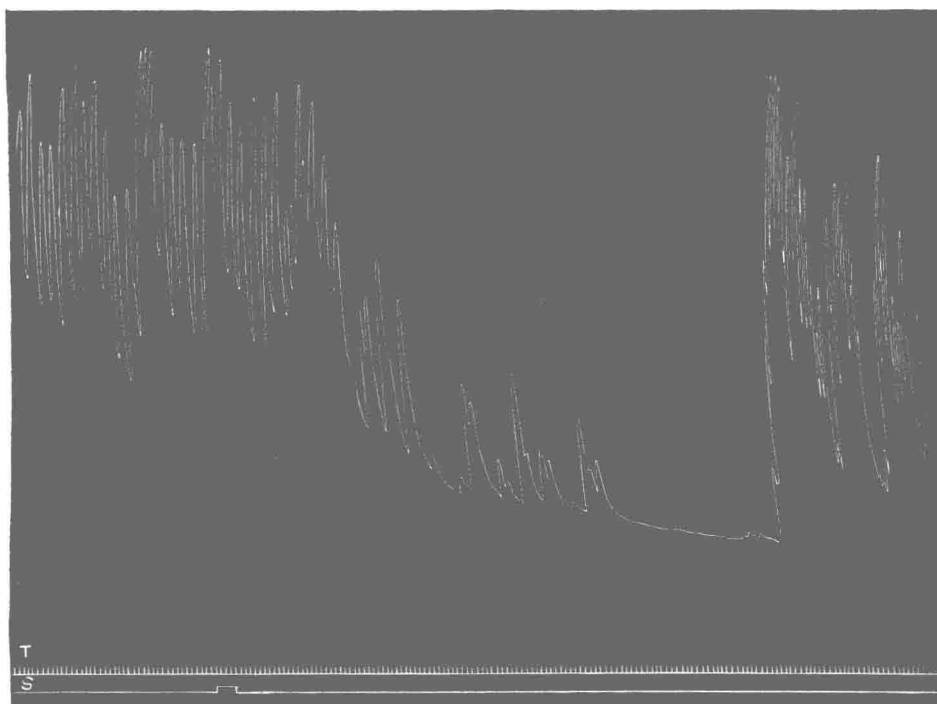


TEXT-FIG. 18. Effect of asphyxia on arterial pressure in the decapitate preparation (J. G. Johnstone and C. F. Krige). A.P., carotid pressure by Hg manometer; Z, zero-line of arterial manometer; T, time in 2" intervals; S, signal marking the time during which the ventilation-pump was disconnected from the tracheal cannula; it will be seen that it was reconnected very soon after the 2nd and profunder stage of heart-block (1 ventricular beat to 3 of auricle) had set in.

ANNOTATION

Obs. 1. Ringer-Locke fluid is a 'normal saline' for mammalian tissues, isotonic with and resembling in composition the saline contents of mammalian blood plasma. S. Ringer established (1884, *Jnl. of Physiol.* iv, p. 20, and subsequent papers)

the importance of adding certain minute quantities of Ca and K to the 0.6 per cent. NaCl saline fluid then in use as normal for the frog's heart and amphibian tissues. For mammalian tissues, especially the heart, F. S. Locke (1901) devised a saline



TEXT-FIG. 5. Exsected piece of ileum (cat) in Ringer-Locke fluid at 35° C. Pendular and 'tonic' waves of contraction inhibited by adrenal extracts (E. Woods). *t*, time in 4" intervals. *s*, signal indicating when adrenal extract was added.

having a content of Na, Ca, and K in quantities normally present in rabbit's blood-serum (*Jnl. of Physiol.* xxxvi, p. 220, 1907), and this is now in general use in physiological laboratories; it is what is here referred to as 'Ringer-Locke'. Its composition is:—

0.015 p. cent.	sodium bicarbonate	} in dis- tilled water.
0.024	„ calcium chloride	
0.042	„ potassium chloride	
0.92	„ sodium chloride	

The water should be distilled in apparatus of glass, not metal, the merest traces of certain metallic ions being poisonous to many living tissues, e.g. heart. When used for perfusing the heart, Locke has shown that the addition of 0.1 per cent. glucose is an improvement.

Obs. 2. 'Adrenalin' is the name adopted for the active principle extracted from the medulla of the adrenal gland. The physiological powers of such extracts were dis-