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THE EFFECT OF CERTAIN ANAESTHETICS ON THE ACTIVITY OF SMALL MOTOR FIBRES SERVING THE HIND LIMB OF THE RAT

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In their recent study of the activity in small motor fibres in the nerve supply of the gastrocnemius muscle of the decerebrate rabbit, Diete-Spiff & Pascoe (1959) noted that certain volatile anaesthetics, namely, ether, ethyl chloride, chloroform and trichlorethylene had a strong stimulatory effect, whereas chloralose, hexobarbitone sodium, and thiopentone sodium depressed the discharge. In their experiments urethane was found to act as a stimulant both in the decerebrate animal and in intact animals already anaesthetized with urethane. It seemed of interest to investigate further the relation between these effects and the simultaneously produced changes in reflex excitability in alpha and gamma fibres.

In the past nearly all the work on the mammalian small motor fibres has been carried out on the cat, and a number of reflex responses, both spinal and supraspinal have been described in the decerebrate, spinal or lightly anaesthetized animal (Hunt, 1951; Granit, Job & Kaada, 1952; Eldred & Hagbarth, 1954; Hunt & Paintal, 1958). In the present experiments many of the procedures which have been used to elicit small motor fibre responses in the cat have been tried on the lightly anaesthetized rat, and certain of these which have been found to produce reflex effects with regularity have been selected and used to follow the changes which occur when anaesthetics are given to the lightly anaesthetized animal. Preliminary reports of part of this work have already appeared (Andrew, 1959, 1960).

METHODS

The experiments were performed on twenty-six adult rats. Anaesthesia was induced with trichlorethylene vapour and maintained by intraperitoneal injection of urethane solution, 25 g/100 ml., 4 ml./kg body weight. Further injections were given as necessary. In four experiments, pentobarbitone sodium, and in two other experiments thiopentone sodium were used instead of urethane as the basal anaesthetic. The level of anaesthesia was controlled so that it was deep at the beginning of the experiment during dissection and was permitted to lighten later when nerve activity was examined. In some of the animals flexion

withdrawal reflexes could be aroused in the hind limb by stimulation of the toes, but there was no stretch reflex activity in the hind limb extensor muscles.

Dissection. Nerve dissection was carried out under liquid paraffin. A binocular dissecting microscope was used. As the rat's leg is rather small, there was usually not enough skin available to form the raised edges of a pool of liquid paraffin over the nerve and muscles to be dissected; it was found convenient to fit an oiltight silver-foil boundary wall to the wound cavity with a depth of 1 cm. The limb was not denervated, and in order to disturb the muscle innervation as little as possible recordings were made usually from the central ends of small intramuscular nerve filaments. Where recordings were made from one of the larger trunks, e.g. the peroneal nerve, the epineurium was removed with scissors without interrupting the nerve. The perineurium was then slit longitudinally with needle points and slender nerve filaments picked off the main bundles. In some preparations, in order to loosen the bundles of nerve fibres, a small volume of hyaluronidase solution (about 100 i.u. dissolved in a fraction of a millilitre of Locke's solution) was run into the opened nerve trunk.

Recording. The electrodes were bright silver wires, and were connected to conventional capacity-coupled amplifiers and thence to cathode-ray oscillographs and loudspeaker. The action potentials were recorded on moving bromide paper.

Inhalation. The head of the rat was inserted into the open end of a Perspex box 7 cm long and 4 × 4 cm cross-section. A tube entered the box opposite the mouth of the animal. In experiments with nitrous oxide and oxygen mixtures, and bromochlorotrifluoroethane (Fluothane; Imperial Chemical Industries) and air mixtures, the gas mixture was passed into the box and escaped with expired gases through the space between the animal's neck and the mouth of the box. To produce anoxia the air in the box was diluted with nitrogen in the same way. The responses to ether, ethyl chloride, chloroform and trichlorethylene were obtained by placing cotton-wool soaked in the anaesthetic in the box and partly withdrawing the animal's head. Tracheal cannulae were not used, and on the few occasions that respiratory obstruction developed the animal was discarded.

Nomenclature. In the literature, the efferent fibres which have been proved or presumed to operate the intrafusal muscle fibres have been referred to as gamma efferents, small motor fibres, fusimotor fibres, spindle motor fibres and intrafusal motor fibres. In this paper the terms gamma efferents or small motor fibres will be used. The vasomotor efferents, although detectable in many of the nerve filaments used in this work, are not included in this category.

RESULTS

Of the basal anaesthetics that have been tried, urethane has proved to be the most reliable; there is a large margin of safety with increasing dosage, it does not depress respiration unduly and the anaesthetic lightens slowly and in a predictable way throughout an experiment lasting several hours. Thiopentone sodium, pentobarbitone sodium and chloralose were given trials but found less satisfactory. The following description of reflex activity in gamma efferents refers therefore primarily to the rat lightly anaesthetized with urethane; the results with thiopentone sodium and pentobarbitone sodium as the basal anaesthetic were qualitatively similar. No useful results were obtained with chloralose.

A group of reflexes has been selected to study the action of anaesthetics given in addition to the basal anaesthetic. They are all easily elicited by natural forms of stimulation (that is, they do not involve electrical stimula-

tion of nerve trunks) and they are differentially sensitive to additional anaesthetic given either by inhalation or injection. Table 1 gives a summary of these reflexes and includes for completeness the reflex response to anoxia and certain inhaled anaesthetics.

TABLE 1. Reflexes operating on gamma efferents used in the present study

	Afferent stimulus	Recording site	Effect
(*a*) Spinal	Toe pinch, ipsilateral	Flexor muscle nerves	Excitation
		Gastrocnemius nerve	Inhibition
	Toe pinch, contralateral	Gastrocnemius nerve	Excitation
	Heel pinch, ipsilateral	Gastrocnemius nerve	Excitation
(*b*) Supra-spinal	Touch in ext. auditory meatus (head-shake reflex)	Limb muscle nerves	Phasic excitation
	Pinna pinch	Limb muscle nerves	Prolonged excitation
	Inhaled ether, ethyl chloride, chloroform, trichlorethylene	Limb muscle nerves	Excitation
	Anoxia	Limb muscle nerves	Excitation

In the description of the results it has been assumed that, in general, the relative sizes of action potentials in records of the activity of a group of nerve fibres are related to the nerve-fibre diameters; the validity of this assumption in the case of efferents to skeletal muscle has been examined and supported by Hunt (1951). In the rat, when electrodes are placed on the central end of a nerve trunk supplying one of the larger limb muscles, it is usually not possible to detect the impulses in the gamma fibres. These become detectable when the nerve is split into very slender filaments. In this situation there is usually little difficulty in distinguishing, on the basis of action-potential size, between alpha and gamma fibre action potentials. When, however, records are made of efferent activity in small intramuscular nerve branches, the results suggest that there is less difference in fibre diameters. This is conjecture, but in any case it is convenient to retain the terms alpha and gamma, even though in this recording position they may not be accurate descriptions of fibre diameter. In these situations the main clues to identification are found in the temporal pattern of action-potential activity.

Toe-pinch reflexes. The receptive field extends over all five toes and the adjacent skin of the sole of the foot. The pinch was applied manually with blunt forceps. The excitation of the gamma fibres to the flexor muscles and the inhibition of the active gamma fibres to the gastrocnemius muscle on the ipsilateral side is assumed to be part of the flexion withdrawal reflex, and it occurs irrespective of whether the anaesthetic level prevents the alpha motoneurones from discharging. The response of a tonically discharging gamma fibre of a flexor muscle and the beginning of the discharge in an alpha fibre are shown in Fig. 1. The excitation of gamma

fibres of the contralateral limb appeared to affect both flexor and extensor muscles.

Heel-pinch reflex. The receptive field extends over the heel of the ipsilateral foot and includes the hairy skin over the Achilles tendon. There is a quite sharp demarcation line between the heel zone of the sole, which causes excitation of the gastrocnemius gamma efferents, and the toe zone, which causes inhibition of the same fibres. Exploration with a probe while recording from the peripheral end of the sural nerve showed that both zones are within the innervation field of this nerve. In some animals very few of the gastrocnemius gamma fibres maintained a tonic discharge; however, their presence in a nerve filament could be revealed by starting a short discharge by pinching the heel region. The beginning of a discharge in two gamma fibres to the lateral gastrocnemius muscle in response to heel-pinch can be seen in Fig. 2(*a*).

Head-shake reflex. If a probe is moved gently in the opening of the external auditory meatus, the animal shakes its head after a short latency, presumably in an attempt to dislodge the foreign body. During the oscillatory movements of the head a short volley of impulses is discharged in gamma fibres to hind-limb muscles. In some instances larger fibres become active also. Presumably this discharge forms part of the postural compensation of the limbs during the shaking movements of the head. An example is given in Fig. 3.

Pinna-pinch reflex. Pinching the pinna with forceps produces, after a brief interval, a general excitation of limb gamma fibres which usually extends beyond the duration of the stimulus. In some animals alpha fibres were also stimulated and slight movements of the limbs occurred. The pinch may be enough to start a tonic discharge in a hitherto inactive fibre. The receptive zone is confined to the pinna itself, pinching the surrounding skin is ineffective. An example is given in Fig. 4(*a*).

Anoxia. The stimulant effect of anoxia on gamma fibres is a general one and is exerted supraspinally. It is usually delayed until anoxia is severe and corresponds in time to the massive discharge in the sympathetic fibres and protrusion of the eyeballs. The supraspinal nature of this excitation has been shown in the cat by Schulte, Busch & Henatsch (1959).

Resting discharge. There appeared to be a large variation between different animals in the number of tonically discharging gamma fibres. As a general rule it seemed that the lighter the anaesthesia, the larger the number of active fibres, the more labile the discharge rate, and the greater the reflex accessibility of the gamma motoneurones to sensory stimulation. The discharge rate in some preparations underwent spontaneous changes of frequency, a cyclical rise and fall of frequency with a periodicity of a

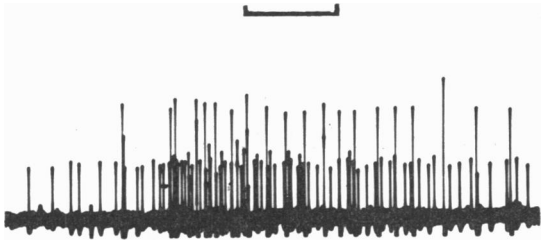

Fig. 1. The responses to ipsilateral toe pinch in group of fibres serving a hind-limb flexor muscle. The fibre with the small action potential which discharged throughout the record was tonically excited when ethyl chloride was inhaled by the animal. The fibre with the largest action potential, which was presumed to be an alpha fibre, was not caused to discharge tonically by ethyl chloride inhalation and gave reduced response to toe pinch after several minutes of inhalation and after the disappearance of head-shake and pinna-pinch responses. Time marker, 1/5th sec.

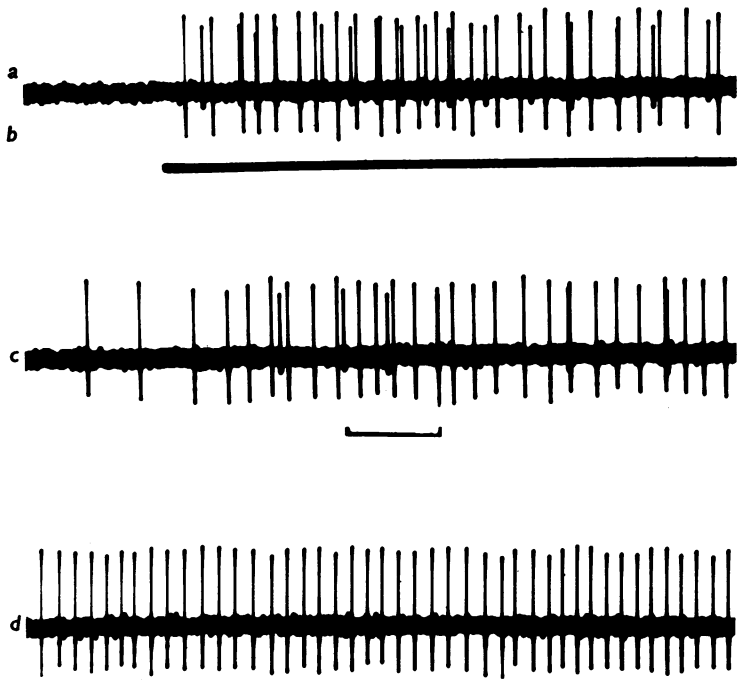

Fig. 2. Records (*a*), (*c*) and (*d*) are from the same gamma fibres dissected from the nerve to the lateral gastrocnemius muscle. The signal marker (*b*) indicates pinch applied to the heel of the foot and applies to the three records. (*a*) shows the control excitation. (*c*) shows the much reduced response which modulates the continuous discharge after 45 sec of inhalation of ethyl chloride. (*d*) shows the unresponsiveness of the tonic discharge to the same stimulus after 2½ min inhalation. Time marker, 1/5th sec.

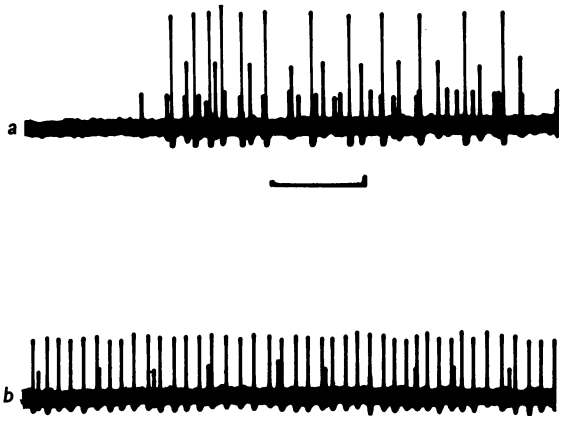

Fig. 3. Records (*a*) and (*b*) are from the same filament dissected from the central end of the peroneal nerve. (*a*) shows the short phasic excitation which occurred in three fibres during the oscillatory movements of the head-shake reflex. (*b*) After 2½ min of inhalation of trichlorethylene vapour the intermediate sized fibre had begun to discharge continuously and at about this time the head-shake reflex failed to influence the discharge in all three fibres. The largest fibre could still be activated by the flexion withdrawal reflex, but there was no phase of tonic excitation due to the anaesthetic: it was presumed to be an alpha fibre. The smallest fibre was tonically excited but to a lesser extent than the intermediate sized fibre. Time marker, 1/5th sec.

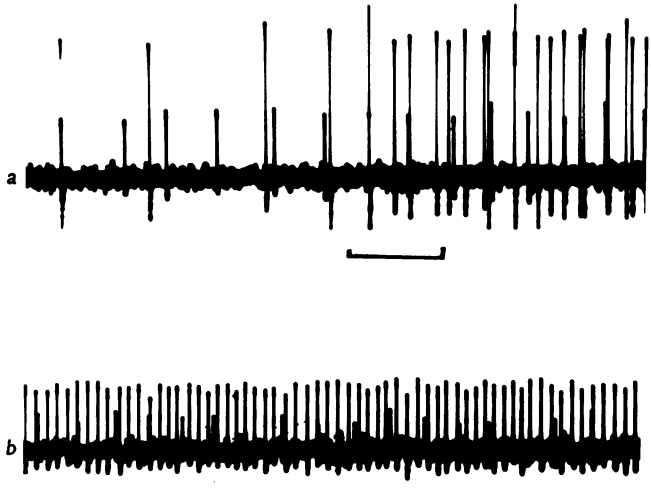

Fig. 4. Records (*a*) and (*b*) are from the same filament dissected from the central end of the peroneal nerve. (*a*) shows the increasing activity as the pinna was pinched, both fibres were accelerated. (*b*) Shows the activity after 2 min of ethyl chloride inhalation. The smaller fibre seen in record (*a*) was now discharging continuously at 50 impulses/sec and another smaller fibre had been recruited. Time marker, 1/5th sec.

fraction of a minute was occasionally seen. In these rather active preparations, a loud sound would sometimes cause a great increase in activity and the recruitment of hitherto inactive gamma fibres.

The effects of additional anaesthetic

Urethane. In four experiments the effects of a series of doses of urethane on the reflex and tonic activity of alpha and gamma fibres were examined. The injections were intravenous in two and intraperitoneal in the others and were continued until respiration stopped. The dose required to produce respiratory arrest in an animal that has been anaesthetized for some hours is relatively large and in these experiments was 370, 625, 650 and 875 mg. The temporal order of effects as the dosage of urethane was increased was as follows: resting discharge stopped, the supraspinal reflexes, i.e. head-shake, ear-pinch and the response to ethyl chloride disappeared, alpha-fibre component of flexor reflex disappeared, and finally the gamma response to toe-pinch (ipsilateral). At no stage was any excitation of gamma fibres detected. In one of these animals there was a slight reflex movement of the muscles operating on the pinna when the latter was pinched; this movement persisted after the excitatory linkage to the limb gamma motoneurones had been interrupted.

Inhalation anaesthetics, type 1: ethyl chloride, ether, trichlorethylene and chloroform. The characteristic feature of this group was that they produced a phase of progressive excitation during which the frequency of the tonic discharge rose to a maximum. The response occurred with each of the three basal anaesthetics used, namely urethane, pentobarbitone sodium and thiopentone sodium. A description will be given first of a typical response to trichlorethylene. Usually four phases could be recognized. During the first half minute of inhalation there were signs of arousal such as movements of the vibrissae and changes in respiratory rhythm; at this time the gammas accelerated slightly and tonic discharges in alpha fibres sometimes began. This phase was absent in some animals. Then followed 3 or 4 min during which alpha activity stopped and resting discharges, if any, in gamma fibres ceased. At about the fourth or fifth minute, the phase of excitation in gamma fibres began, and a quite regular tonic discharge of rising frequency occupied the next few minutes. The discharge then ceased abruptly or continued for a short time as a series of high-frequency trains of impulses and then ceased. By this time the animal was deeply anaesthetized; the head-shake and pinna-pinch reflexes disappeared during the phase of excitation. The extinction of the heel-pinch reflex before the end of the phase of tonic excitation of the gamma fibres is shown in Fig. 2. The toe-pinch response in nerves to flexor muscles was rather more resistant, and some modulation of the discharge could be heard at the end of the

excitation phase. During the ensuing few minutes after the rat was returned to breathing air the gammas might pass back through the excitation phase and the reflexes returned in the reversed sequence. The maximum frequencies achieved during the phase of excitation were variable, and the range extended from a change from zero–28 impulses/sec to zero–110 impulses/sec; that is, within the normal limits of frequencies observed when gamma fibres are activated reflexly. In recordings from multi-fibre preparations it was seen that the phase of excitation did not

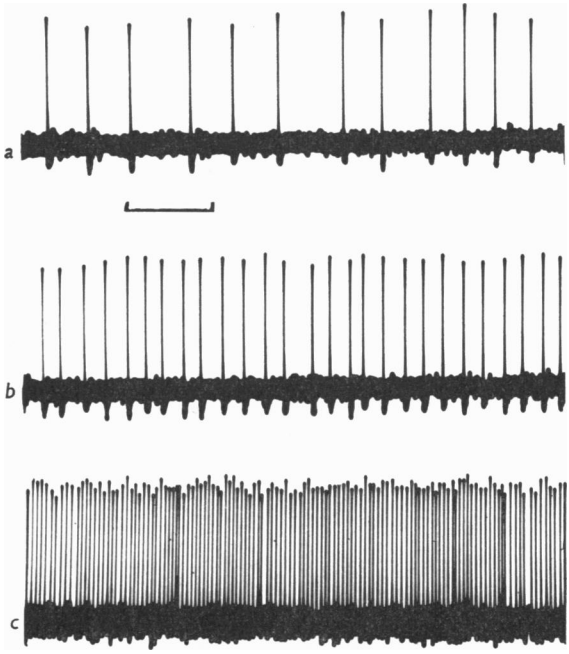

Fig. 5. Response to the inhalation of ethyl chloride vapour in a single gamma efferent in an intramuscular nerve branch serving the medial gastrocnemius muscle. Control record (*a*) shows the resting discharge, 10 impulses/sec; (*b*) after 60 sec inhalation, discharge rate 22 impulses/sec; (*c*) after 80 sec inhalation, discharge rate 105 impulses/sec. Time marker, 1/5th sec.

begin synchronously in all fibres and towards the end of the phase some became quiescent before others. The response to ethyl chloride was more rapid, the tonic excitatory phase began in 1 min or less but was similar in form. In one experiment the heel-pinch reflex was tested every 10 sec and it was extinguished after 40 sec inhalation. Ether and chloroform vapour were used in two experiments only, they gave results similar to trichlorethylene. In four trials two or more type 1 anaesthetics were given in sequence to make sure that the same fibres partook in the responses to the different anaesthetics. The acceleration of the tonic

discharge in a gamma fibre during inhalation of ethyl chloride is shown in Fig. 5 and plotted graphically in Fig. 6.

Inhalation anaesthetics, type 2: bromochlorotrifluoroethane. This anaesthetic was found to be very rapid in its action on the gamma reflexes but it did not produce a phase of tonic excitation. When it was given in a similar way

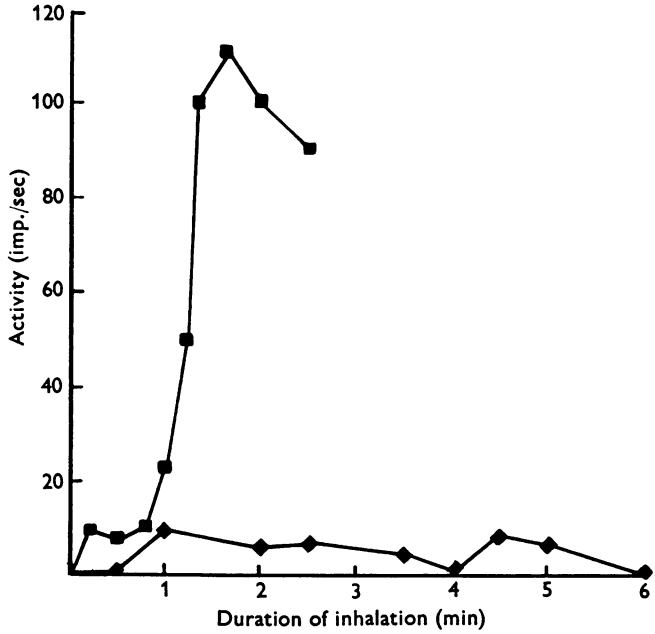

Fig. 6. Activity in a gamma fibre in an intramuscular nerve branch in the medial gastrocnemius muscle. ■, the response to ethyl chloride vapour; ◆, the activity in the same fibre during the inhalation of a mixture of 90 % nitrous oxide and 10 % oxygen.

to trichlorethylene (that is, it was allowed to evaporate from cotton-wool in the open-ended box containing the head of the animal), it extinguished the gamma reflexes within half a minute, and there was no phase of excitation. On return to air breathing the heel-pinch reflex reappeared after 4 min and the ear-pinch and head-shake reflexes after 6 min. When the animal was breathing a 4% (v/v) air mixture and the heel-pinch reflex was tested every 10 sec, it was found that the reflex was affected after 20 sec and extinguished after 80 sec. There was no phase of excitation.

Nitrous oxide. This anaesthetic was tried in three concentrations on three animals, namely 100%, 90% nitrous oxide +10% oxygen, 80% nitrous oxide + 20% oxygen. When it was given as the pure gas, while recording from a fibre that had shown a response to ethyl chloride there was no tonic response and respiratory arrest occurred after 2 min inhala-

tion. At this point there was head-shake movement but no gamma excitation and a reduced heel-pinch response. After recovery the gamma response to anoxia produced with nitrogen was tested and excitation occurred after 1¼ min. Inhalation of 10% O_2 + 90% N_2O produced no tonic excitation but there was an interruption of supraspinal effects; after 5 min inhalation the head-shake reflex had gone and there was no response to ethyl chloride, but the toe- and heel-pinch reflexes remained. Figure 6 shows the response of the same fibre first to ethyl chloride and then, after a pause for recovery, to 90% nitrous oxide + 10% oxygen. The effects of 80% nitrous oxide with 20% oxygen were qualitatively similar. It seemed from these experiments that nitrous oxide interrupted the pathways whereby anoxia, ethyl chloride, and the head-shake and ear-pinch reflexes normally excited the spinal gamma motoneurones, but did not interfere with the spinal gamma response to foot stimulation.

DISCUSSION

Some species differences in the reflex responses to ear stimulation are evident. In the lightly anaesthetized rat the pinna and the external auditory meatus are the most reflexogenic zones on the head. On the other hand, Diete-Spiff & Pascoe (1959) report that in the rabbit the skin of the ears was the only region from which gamma excitation was not obtained. As has been shown by Granit *et al.* (1952), twisting the pinna in the cat has a potent effect on lumbar gamma activity, either causing acceleration of discharge or an inhibition followed by an acceleration. However, in the present rat experiments ear-twist was ineffective but ear-pinch was always excitatory to the limb gamma efferents, and in some preparations, to alpha fibres as well. In the anaesthetized rat the scratch reflex does not occur after ear-pinch, but slight movements of the ipsilateral forelimb were seen rarely. Sherrington (1917) included the head-shake reflex in his description of the ear reflexes of the cat, but later workers do not appear to have studied its gamma fibre component to the limbs. Certainly one would expect that the oscillatory movements of the head would be accompanied by phasic adjustments of the innervation of limb muscles in order to preserve equilibrium.

The surfaces of the foot which either excite or inhibit the gamma efferents serving the gastrocnemius muscle of the rat are similar to those described by Eldred & Hagbarth (1954) for the cat, except that the excitatory zone in the rat extends rather more on to the sole of the foot. The fact that the sural nerve contains afferents from these two zones of opposite action on the gamma motoneurones of the gastrocnemius muscle suggests that rather variable results will follow the electrical stimulation of the whole nerve trunk. Urethane was used as the basal anaesthetic in

most of the experiments described in this paper, and for this reason care was taken to check whether it was a stimulant to the gamma system, as has been reported in the rabbit by Diete-Spiff & Pascoe (1959). No excitation was seen at any stage, but of course these tests refer only to doses additional to that required to produce light anaesthesia. It is difficult to predict what the level of gamma activity is in the intact unanaesthetized animal. The activity in the decerebrate unanaesthetized preparation is variable, and if rigidity is present the gamma activity may follow the spontaneous changes in rigidity (Hunt, 1951). A feature which was frequently observed in the present study was that as the anaesthesia lightened the level of gamma activity became more labile, was easily influenced by an increasing range of sensory stimulation and in some instances was subject to apparently spontaneous rhythmic shifts of activity level. Thus, it may be that in the intact unanaesthetized animal, the level of gamma activity is very labile, being increased in states of alertness or in anticipation of a movement. The familiar difficulty of distinguishing between small and large motor fibres was present throughout this work. The small fibres could rarely be detected except in very slender nerve filaments. Furthermore, when recording from intramusclar branches the activation of alpha fibres in nearby innervated muscle led to electromyographic activity which could be heard on the loudspeaker and to slight movements which could be seen through the dissecting microscope. This information was useful but not conclusive, since alpha activity does not necessarily begin simultaneously in all parts of the muscle. The use of action-potential size (Hunt, 1951) is satisfactory if one is permitted to suspend judgement in preparations where the ratio of action-potential sizes is small. These situations arise frequently, and there is a need for simple distinguishing tests. It is possible that the use of a quickly-acting volatile anaesthetic such as ethyl chloride may be of value, but first it must be decided whether all small motor fibres are excited, or whether a group of some significance functionally alone is stimulated. Certainly several filaments which had been predicted from other features to be gamma efferents failed to respond to ethyl chloride and trichlorethylene. Another feature which is of interest is the great range of observed fibre response. In some fibres the frequency was doubled before it ceased, in others the effect was much greater, e.g. an increase from zero to 100 imp./sec. If this range in the extent of control is genuine and not due to some uncontrolled variable in the experimental procedure, one might expect that some gammas would be beyond the control entirely.

In Fig. 5 the signal-to-noise ratio is unusually large for a gamma fibre; this is due to the use of a particularly slender nerve filament. This is of importance here to show that it is the record from a single active fibre,

since constancy of action-potential size together with regularity of discharge, if found together for several seconds, exclude the possibility that the record is made up of the activity of two or more fibres. Constancy of action-potential size can only be obtained if there is a large signal-to-noise ratio.

It is not clear from these experiments whether the excitatory effect of the type 1 volatile anaesthetics is due to a direct central action or whether it is due to reflex arousal caused by sensitization of sensory endings. Robertson, Swan & Whitteridge (1956) have shown that the threshold of carotid baroceptors is lowered by inhaled ether, chloroform and trichlorethylene. Whitteridge & Bülbring (1944) found that the sensitivity of pulmonary stretch endings was increased and Matthews (1933) detected an increase in excitability of muscle endings during induction of chloroform anaesthesia. Considerations which do not favour this second possibility are, first, that Schulte, Henatsch & Busch (1959) have shown that an increased inflow from the carotid sinus in the cat causes an inhibition of the lumbar gamma motoneurones, and secondly, that with trichlorethylene the main excitation occurs at a stage when other sensory influences have little effect, i.e. when the depth of anaesthesia interrupted sensory connexions with the gamma system.

SUMMARY

1. A study has been made of motor discharges in alpha and gamma fibres to the hind limb of the lightly anaesthetized rat. A group of reflexes which influence gamma activity is described.

2. Three anaesthetics have been used to produce the light basal anaesthesia, namely urethane, pentobarbitone sodium and thiopentone sodium.

3. The effects of additional doses of anaesthetic, given either by inhalation or injection, on the resting discharge and the reflex excitability of the gamma and alpha fibres has been examined.

4. The inhalation anaesthetics have been divided into two groups. The first includes ethyl chloride, trichlorethylene, ether and chloroform. The second includes bromochlorotrifluoroethane and nitrous oxide. Anaesthetics of the first group cause a tonic excitation of gamma efferents and a simultaneous interruption first of supraspinal and then of spinal reflexes. Anaesthetics of the second group have a similar effect on the reflexes but do not produce a tonic excitation.

I wish to thank Professor G. H. Bell for his interest in this work.

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