endings lie, thus stretching the endings in much the same way as an externally applied stretch. The dynamic fusimotor fibres excite only the primary endings, and not the secondary endings, and they have the interesting action of making them yet more sensitive than normal to velocity stimuli. The mechanism of this action is not known. The static fibres do not have this action on the primary ending even though they excite it just as powerfully when the muscle is at a constant length. Very recently, single living muscle spindles have been observed under the microscope while their motor fibres are being stimulated. This has shown that the contractions produced by the static fibres are rather quicker than those produced by the dynamic fibres, suggesting that the two kinds of intrafusal muscle fibre have rather different properties.

Function

The precise functions of muscle spindles are still far from clear, though it is fairly certain that neither they nor the tendon organs contribute to conscious sensation. In a general sense it is perfectly proper to say that they serve as a feed-back pathway for regulating the length of a muscle, but important features of this regulation remain to be discovered. The tendon jerk reflex is certainly due to the tendon cap exciting the primary endings of the muscle spindles, and these then reflexly excite the motoneurones of their own muscle, so that the muscle contracts. This is an example of the 'stretch reflex' in which a muscle contracts in response to stretch of itself. A tendon tap or muscle stretch will also excite the tendon organs and the secondary endings of the spindle, but neither of these produces a reflex contraction of its own muscle. It has been suggested that some voluntary muscle contractions may be produced rather indirectly by central nervous activity impinging in the first place on the fusimotor neurones rather than on the ordinary motoneurones. Fusimotor activity leads to contraction of the intrafusal fibres with excitation of the primary endings. In their turn these would excite the ordinary motoneurones of their own muscle leading to a 'stretch reflex' contraction of the muscle. Certain theoretical advantages have been thought to follow from this mode of activation of muscle and the scheme has been called the 'follow-up length servo hypothesis', but recent work makes it look rather less attractive than before and there is no very strong evidence that movements are ever solely produced in this way. It is better to confess that we are still largely in the dark about the precise uses made by the nervous system of the information from the muscle spindles.

OTHER RECEPTORS

In addition to muscle spindles and tendon organs, muscle may contain a large number of free afferent nerve endings which arise from the smallest medullated nerve fibres and from non-medullated nerve fibres. These do not respond on stretch of a muscle nor on its contraction but they are excited by squeezing. They may be simply pain receptors responding to noxious stimuli, but it is still not established that they are all of one kind and that this is their sole role. There are also a few 'onion-like' encapsulated Pacinian corpuscles in and around muscles. The function of these may be to mediate 'vibration sense', for they are very sensitive to vibration.

Spinal Reflex Action

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Reflex action has been defined as the subconscious response resulting from a sensory stimulus. Such a definition is sometimes taken to imply that no conscious control can be exercised over spinal reflex activity, but this is not the case. Imagine, for example, a person inadvertently touching a hot plate with his hand. As a result of the painful and unexpected stimulus the hand would be rapidly withdrawn, an example of the flexor reflex. However, if the plate is of the same temperature but for some reason it is necessary to pick it up, it is possible to do so. The sensory stimulation to the skin is the same, but the latent reflex withdrawal has been overridden by higher centres. This simple illustration stresses the lability of the spinal reflex, a characteristic well appreciated by Sherrington but now often overlooked. It will be the purpose of this short article to attempt to demonstrate the shortcomings of thinking in terms of 'simple' spinal reflex arcs, and to emphasise the complexity of spinal organisation.

THE SYNAPSE

One characteristic of all spinal reflexes is the presence of one or more synapses along their course. A synapse is a functional region between two neurones at which there is no protoplasmic continuity. The electron microscope has demonstrated a variety of synaptic forms, in some of which the surface membranes of the pre- and post-synaptic cells appear to fuse, but the commonest appearance is that of a well-defined synaptic cleft ranging from 50°-200° A in width separating the neurones. Often the termination of the presynaptic cell shows a bulbous expansion, the synaptic knob. In the mammal, transmission from one neurone to the next is believed to be accomplished by the release of a chemical substance from the pre-synaptic terminals which, diffusing across the synaptic cleft, produces an alteration in the permeability characteristics of the adjacent post-synaptic membrane. With the electron microscope it is often possible to see small vesicles within the pre-synaptic nerve terminals, and it is thought that these may contain the transmitter substance. In this respect there is a marked resemblance to the situation at the motor end-plate where the motor axon terminals appear to contain vesicles which are thought to contain acetylcholine, the mammalian neuromuscular transmitter. However, in the case of the synapses within the nervous system the nature of the chemical transmitters is not known, save in a few specialised sites. Whatever the chemical nature of the transmitter substances may be, it is believed that any one neurone can only manufacture one type of transmitter and that this will be produced at all the terminals of the neurone.

Functionally these are two types of synapse, excitatory and inhibitory, the distinction depending upon whether an impulse in the pre-synaptic fibre increases or decreases the excitability of the post-synaptic cell. A single nerve impulse arriving along the pre-synaptic terminal of an excitatory synapse causes a transient small depolarisation of the post-synaptic cell membrane due to an alteration in its permeability characteristics. This small depolarisation, a unitary excitatory post-synaptic potential (E.P.S.P.) is typically 0.25-1.0mV in amplitude, lasts a few milliseconds, and during this time renders the post-synaptic cell more likely to discharge a nerve impulse. However, since a typical neurone has to be depolarised by some 10-15 mV before discharge takes place it is apparent that a single excitatory presynaptic impulse constitutes only a subliminal stimulus. It is typically by the summation in both time and space of many such subliminal stimuli that the firing threshold of the post-synaptic cell is reached. The 'summation' of the various excitatory influences each brought about by an active synapse on different parts of the cell soma occurs in the initial segment of the axon since it is here that the current leaving the cell first reaches the critical density. It is therefore

from the initial segment that the post-synaptic cell nerve impulse arises—if indeed it arises at all.

It will have been noted above that the amplitude of the depolarisation produced by a single pre-synaptic impulse is variable. This variability has at least three causes. Firstly, the site of the synaptic contact on the post-synaptic cell soma is important; the further away along a dendrite it occurs the less influence it exerts. Secondly, it appears probable that synapses are not rigidly fixed but that the exact geometrical relationship between the pre- and post-synaptic structures may vary from time to time. Such positional changes will vary the efficacy of pre-synaptic impulses. Thirdly, the amount of excitatory chemical transmitter liberated by a single pre-synaptic nerve impulse in one pre-synaptic terminal may also vary. The most important cause of such variation may be what Eccles has named 'pre-synaptic inhibition'. Pre-synaptic inhibition occurs when an additional neurone influences the pre-synaptic axon in a manner which causes it to release a smaller than normal amount of transmitter substance per impulse (and therefore exert a small excitatory effect on the post-synaptic cell). The extent and importance of pre-synaptic inhibition within the central nervous system is not yet known, but it may be considerable.

An inhibitory synapse is one at which an impulse in the pre-synaptic fibre leads to a transient hyperpolarisation and therefore reduced excitability of the post-synaptic cell. Again the effect is believed to be chemically mediated and the transient potential change is known as an inhibitory post-synaptic potential (I.P.S.P.). The amplitude and time course of a unitary I.P.S.P. is very similar (but of opposite polarity) to that of a unitary E.P.S.P., and therefore the simultaneous arrival of one excitatory impulse and one inhibitory impulse on the surface of a post-synaptic cell leaves the excitability of the cell effectively unaltered. During life post-synaptic neurones within the C.N.S. are being continuously bombarded with both excitatory and inhibitory impulses, the effects of which seem to determine their instantaneous excitability. If there is a net excess of excitatory impulses the post-synaptic cell is depolarised, and if the depolarisation of the initial segment of its axon reaches the critical level and nerve impulse is initiated.

This description of how the mammalian synapse functions is largely due to the brilliant work of Eccles and his colleagues over the past 15 years. While there are certain problems still to be solved there can be little doubt that the basic picture of synaptic transmission is now clear. Unfortunately the clarification of our understanding of the synapse has to some extent been made at the expense of our understanding of reflex activity. This is fortuitious and has occurred largely because in studying the synapse only the simplest reflex paths were used, and the complexity of the connections established by many of the spinal afferents were ignored in the excitement of studying the single neurone. Now that this phase is complete the new knowledge of synaptic transmission must be married to the total organisation of the spinal cord which so fascinated Sherrington.

SPINAL AFFERENTS

Much of the loose thinking which takes place in students' minds regarding reflex activity stems from the use of over-simplified diagrams. It is inevitable that in the early teaching of reflex arcs diagrams have to be used, but too often the diagrams are accepted as anatomical fact. Consider, for example, the monosynaptic reflex arc. This may be represented as a single afferent entering the posterior horn of the spinal cord, crossing directly to a single large anterior horn cell which it synapses and from which springs a large efferent motor fibre. In a diagram designed to stress the point that in this particular type of spinal reflex no inter-neurones are present no other connections of the incoming afferent fibre may be shown. Such a diagram, while illustrating a point, is far from anatomical fact. To make but a few of the possible additions, the incoming afferent will

give off collaterals which ascend in the posterior columns. Further collaterals will synapse with interneurones which pass to synapse with the motoneurones of antagonistic muscle groups. The single incoming afferent will synapse not with a single large anterior horn cell but with each cell of the motoneurone pool. The motor axon of the large anterior horn cell is likely to give off a Renshaw recurrent collateral—and so one could go on. The point to be stressed is that it is the very complexity of the interconnections within the spinal cord which are at the root of its behaviour. No truer phrase has been written than that stating that the simple spinal reflex arc just does not exist!

Turning now to the afferent inflow into the spinal cord, three major groups of fibres exist, namely those from the cutaneous surface, those from muscle and tendon, and those from joints. All have their cell body in the posterior root ganglion and enter the posterior horn of grey matter. All make connection either directly or indirectly with higher centres, but the ascending spinal pathways will not be further discussed in this article. However, it should be noted that even at the posterior horn of the spinal cord the first sorting and recognition of sensory inflow is being undertaken in the newly recognised 'pain gate'. The diversity of the central reflex connections of the incoming afferents to the same side of the spinal cord, to the contralateral side and to differing levels of the cord, is enormous. Only the mono-synaptic afferents which arise from the primary sensory end organs in the muscle spindles pass directly to the moto-neurones of the parent muscle and to a lesser extent to the motoneurones of synergistic muscles. Even then, as mentioned above, the influence of the incoming impulses is felt more widely via interneurones. All other afferent fibers, whether originating in skin muscle or joint, make connections with anterior horn cells only via one or more interneurones.

SPINAL INTERNEURONES

The importance of interneurones has only recently been generally recognised. They may be divided into two groups: those that in the waking state are spontaneously discharging, and those that only discharge when critically excited by incoming afferent impulses. It also appears that all inter-neurones come under the influence of descending extra-pyramidal impulses (both excitatory and inhibitory), but the former group of interneurones less so than the latter. For most reflex arcs the interneurones represent the first level of organisational control. It may be imagined that a single afferent fibre making excitatory synaptic contact with a number of interneurones may at a particular time have synaptic transmission facilitated at some junctions and blocked at others as a result of a particular pattern of descending extrapyramidal activity. At another time the position may be reversed. Such behaviour gives the first vague picture of the organisation of reflex excitability being governed and modified by higher centres from moment to moment as opposed to the static inevitability of reflex activity which is so common in many students' minds.

Those interneurones which are spontaneously active typically exert a tonic influence on motoneurones, but the discharge frequencies (which may reach very high rates) may be modified by afferent or descending impulses.

In spite of the complexity of the interconnections there are basic reflex patterns such as the flexor reflex, the crossed extensor reflex, and many others, which represent preferred pathways for certain incoming afferent impulses. The co-ordinated and purposeful nature of a normal reflex response has been repeatedly stressed but its variability in intensity from time to time is too easily forgotten. It is largely the pattern of descending impulses from higher centres that sets the excitability of all the reflex pathways within the spinal cord from instant to instant.

ANTERIOR HORN CELLS

Over the past 20 years the functional significance of the large and small anterior horn cells has become well recog-

nised. The larger cells constitute the neurone of Sherrington's final common path and the nervous elements of the motor units. In the mammal the smaller cells provide the motor innervation of the intrafusal muscle fibres, which in turn set the bias of the primary and secondary spindle sensory end organs. It is thought that the small anterior horn cells may be functionally divided into those which exert a dominant influence on the excitability of the primary sensory end organs and those which exert their main effect on the excitability of the secondary sensory end organs. All small anterior horn cells have their discharge patterns during the waking state determined by the descending pattern of extra-pyramidal impulses. Thus the excitabilities of all the muscle spindles throughout the body are determined instant by instant by the higher centres. Small anterior horn cells receive no monosynaptic afferent connections but may be influenced via interneurones by other incoming afferent fibres, for example those from skin.

The large anterior horn cells may innervate either fast or slow twitch skeletal muscle fibres. It is generally believed that the fast contracting motor units are used for phasic actions, while the slow contracting units are used in main-tained (postural) contractions.

The density and distribution on the motoneurone surface of afferent connections which reach the final common path only through interneurones is not yet known in detail, though it has been suggested that the small afferent fibre projections are organised to produce a flexor reflex. In the case of the largest afferent fibres (the group IA input from the primary sensory end organs in the spindle) which end monosynaptically on anterior horn cells, it is known that, within a synergistic muscle group, there is a larger IA

projection on to anterior horn cells innervating slow motor units than on to fast motor units. This organisation is presumably important in the functioning of the stretch reflex.

Effectively all large anterior horn cells have recurrent collaterals arising from their motor axons. These pass to synapse with interneurones, the Renshaw cells, which exert an inhibitory influence on adjacent motoneurones. Again it has recently been shown that this recurrent inhibition is assymetrically distributed between the anterior horn cells innervating fast and slow skeletal muscle fibres, the slow motoneurones receiving a disproportionally large share of the recurrent inhibition from the collaterals of fast moto-neurones. Whether this enables postural stretch reflexes (maintained via the slow contracting motor units) to be 'turned off' during phasic contractions remains to be seen.

CONCLUSIONS

This brief description of the physiology of reflex arcs has attempted to stress the complexity of the spinal organisation which underlies their operation, and to underline the variability in reflex action which may be introduced by higher centres, or by the concomitant activity of more than one group of afferent inputs. Unfortunately the anatomical complexity renders the production of meaningful diagrams difficult, and for this reason they have been omitted.

It will obviously remain necessary for students to be introduced to the 'simple reflex arc' at some early stage in their training, but every effort should be made to introduce the concept of variability in the excitability of specific reflex arcs and the interaction of different reflex arcs as soon as possible afterwards.