(ii) ontogenetic developmental patterns—relating to the developmental sequences in man.

Therapy techniques use phylogenetic and ontogenetic patterns because they are favoured by the synapses. The older phylogenetic patterns are even more favoured than ontogenetic patterns. J. C. Eccles experiments suggest that each succeeding time a stimulus passes a synapse, the terminal bouton becomes more efficient at producing chemical transmittor and the stimulus passes more easily. If a response can be facilitated once it will be facilitated more easily with each repetition. Repetition has an important place in every technique and the repetitive quality of reciprocal rhythm patterns is very effective because rhythm is also facilitatory.

3. CONCLUSION

Therapists who wish to use facilitatory techniques effectively must be familiar with both the background neurophysiology and with practical aspects of the technique.

Because Miss Rood's technique has such a vast coverage many facets of this fascinating technique have been omitted and readers are recommended to pay careful attention to the bibliography.

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Typing and checking. Miss G. Wilkinson, B.Sc. (Rand).

RECEPTORS IN MUSCLE

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We are normally quite unaware that we have 'sensory' receptors embedded in our muscles, yet they play a continuous part in the nervous control of our movements and they are also involved in the production of symptoms in certain neurological diseases. An example of their potency is provided by the recent finding that when a massage vibrator is firmly applied over the tendon of a normal human muscle, then the muscle contracts, or any pre-existing contraction is made more powerful than before. This occurs independently of any 'volition' on the part of the subject, though by an effort of will he can prevent a movement occurring. In a partially paralysed patient with a spastic paresis the effect of tendon vibration may sum with the effects of volition and allow a 'voluntary' movement to be produced which could not be produced before, and which is much stronger than any movement produced by the vibration alone. The effect of vibration is certainly a reflex from muscle receptors, and those responsible are probably the primary endings of the muscle spindles (see later). Again, if a patient with Parkinson's disease has dilute procaine solution injected at the motor point of one of his muscles, then the muscle will lose its characteristic rigidity even though its voluntary power is fully retained. Procaine injection thus produces a definite improvement in the state of the patient, albeit a temporary one. This effect results from a selective paralysis by the local anaesthetic of the specialised small motor nerve fibres to the muscle spindles, while the ordinary large motor fibres to the main mass of the muscle remain unaffected; local anaesthetics are well known to have a preferential action on small nerve fibres. In spastic children the epidural injection of dilute alcohol can produce a similar alleviation of the hypertonus lasting for a few weeks or months. Any massage of a muscle or manipulation of a joint must excite a variety of intramuscular receptors, and their activity may play a part in the alleviation of symptoms. Thus a knowledge of the nature and behaviour of muscle receptors is essential for a full understanding of much neurological disease and may provide a rationale for certain procedures in physiotherapy, though it must be admitted that a great deal more research needs to be done into 'clinical physiology' before we can claim at all a deep knowledge of such things. The rest of this article outlines the present state of knowledge about muscle receptors. Most of it has been obtained from electrophysiological studies on the cat, but in view of the similarity of their structure it is probable that human receptors behave in much the same way. In both man and cat less than half the medullated nerve fibres in a muscle nerve are ordinary motor fibres to the muscle fibres, while the rest are either motor or sensory to various muscle receptors.

TENDON ORGANS

The simplest of the receptors signalling the mechanical state of a muscle is the tendon organ which was first fully described by Camillo Golgi in 1880 and is now often given his name. Golgi tendon organs lie at both ends of a muscle at the musculo-tendinous junctions where the muscle fibres fuse with the tendon, or with the fascia from which they arise. It is important to realise that tendon organs are not restricted to the anatomically obvious portions of a tendon, and indeed it is doubtful if many at all are to be found in the main tendon. In structure, the tendon organ consists of a simple spray of nerve terminals arising from a large medullated afferent nerve fibre (Fig. 1). The spray lies on the strands of tendon and may be up to 1 mm. long. The function of the tendon organ is to record the tension set up

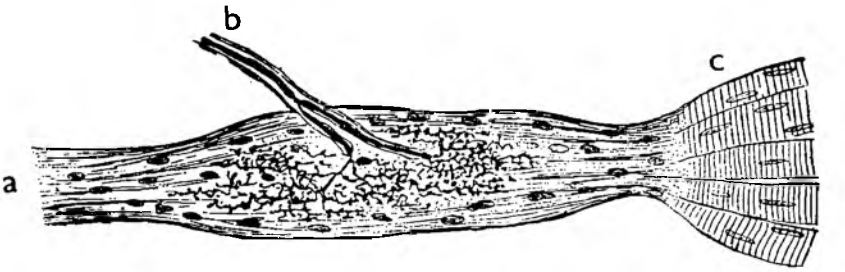

Fig. 1: A tendon organ: (a) tendon; (b) nerve fibre, branching to form tendon organ; (c) muscle fibres.

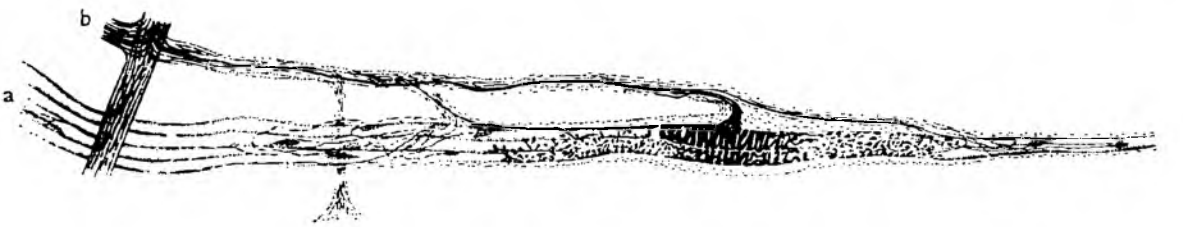

Fig. 2: A muscle spindle: (a) intrafusal muscle fibres; (b) nerve trunk supplying motor and sensory fibres to spindle.

in the small bit of tendon on which it lies, and it thus records the tension set up by the small group of muscle fibres to which this piece of tendon is connected. When a non-contracting muscle is stretched over its physiological range of action the tension in it often does not increase very much, so that the tendon organs usually appear to have a high threshold in response to simple stretching. But when the muscle fibres influencing any particular tendon organ contract there is an appreciable increase in the local tension and the tendon organ is vigorously excited. Accordingly, tendon organs are now often referred to as 'contraction receptors' rather than simply as 'tendon receptors'. When they were believed to have a high threshold to all forms of stimulation the reflex function of tendon organs was supposed to act as a 'safety stop' and to inhibit the motoneurones of a muscle when an unduly high tension was developed in it, thus cutting off any contraction and bringing about a reduction in the tension. While tendon organs may well do this, they are likely also to play a continuous part in the regulation of muscular contraction.

MUSCLE SPINDLES

These highly complicated sensory end-organs are still something of a mystery. Even though they were first observed just over 100 years ago, significant new histological findings have been made with the light microscope in the last few years. Fig. 2 shows a 70-year-old drawing of a muscle spindle stained to show the nerve endings. A muscle spindle consists of a bundle of up to 10 specialised striated muscle fibres around and upon which occur a variety of nerve terminals, both afferent (sensory) and motor. The central part of the muscle spindle has a capsule enclosing some fluid in which the bundle of muscle fibres lies freely. This capsule makes the muscle spindle 'fusiform', and from this it derives its name. The whole structure is usually several mm. long and lies embedded among the ordinary muscle fibres. Fig. 3 shows a simplified diagram of the present view of the structure of a muscle spindle in its central mm. or so. There are two different kinds of muscle fibre within the spindle; they may be distinguished by the arrangement of nuclei in the central region of the spindle and are called the nuclear-bag and the nuclear-chain intrafusal muscle fibres. The nuclear-bag fibres are slightly fatter and have a collection ('bag') of nuclei in their central region. The nuclear-chain fibres have their nuclei arranged in a 'chain' in the central region. Both kinds of fibre have far more nuclei in their central region than elsewhere, and this region

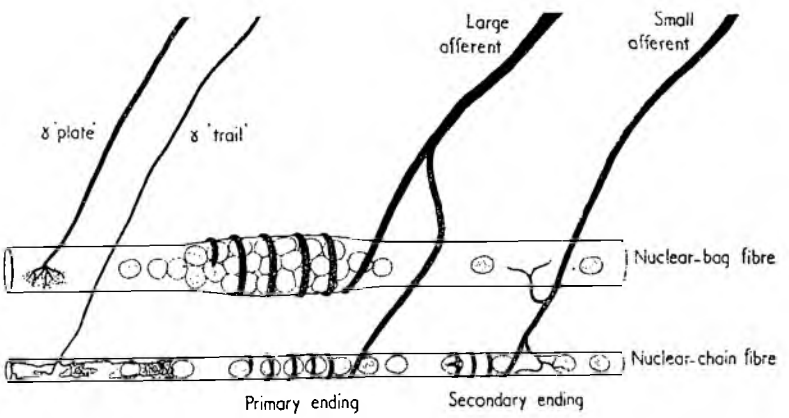

Fig. 3: Simplified diagram of the structure of the central region (about 1 mm.) of a muscle spindle.

is poorly striated so that it probably cannot contract as strongly as the rest of the fibre. Both kinds of intra-fusal fibre are far thinner than ordinary muscle fibres.

There are two distinct kinds of motor nerve fibre to the muscle spindle. The 'γ plate' nerve fibres end in motor endplates which are similar to those on normal muscle fibres. The 'γ trail' nerve fibres end in diffuse motor endings each of which covers a much larger area than a 'plate'; these endings are similar to certain motor endings found in the frog and many invertebrates. (Earlier names which are approximately equivalent to 'γ plate' and 'γ trail' are γ_1 and γ_2 respectively). The 'γ plate' fibres supply preponderantly the nuclear-bag muscle fibres, and the 'γ trail' fibres supply the nuclear-chain fibres preponderantly. It may be noted that the term 'γ' is often applied colloquially to small nerve fibres (around 5μ diameter) to distinguish them from larger nerve fibres, which are called α or β depending on their size. There are usually several motor fibres of each kind supplying a single muscle spindle.

There are also two distinct kinds of afferent (sensory) ending within a muscle spindle. There is always a single 'primary ending' which consists of spirals round the central regions of both kinds of intrafusal muscle fibre, and there are also one or more 'secondary endings' which lie mainly on the nuclear-chain fibres slightly away from their central region. The primary endings are supplied by some of the largest nerve fibres in the body (up to 20μ diameter). The secondary endings are supplied by slightly smaller medullated nerve fibres.

Behaviour

The behaviour of the afferent endings has been extensively studied by recording from single afferent nerve fibres while stretching the muscle and while stimulating single γ motor fibres. Perhaps it should be explained that the phrase 'single fibre' means functionally single and not anatomically single. The functionally single fibre is obtained by exposing the spinal nerve roots by a laminectomy and then splitting them into tiny filaments until only one nerve fibre from the muscle being studied remains in the filament. The nerves to most other muscles supplied by the nerve root are cut so as to avoid any interference from them. The primary and secondary endings of the muscle spindle are both responsive to stretch of the muscle, and for maintained increases in the length of the muscle their discharge, in impulses/sec, is increased by a very similar amount. Their behaviour differs strikingly, however, during a period of stretching of a muscle, say with a constant velocity, when the primary ending fires far more rapidly than does the secondary ending. This is illustrated in Fig. 4 where the frequency of firing of the two kinds of endings is seen to be very similar at the initial and final lengths, but the primary is firing far more frequently during the phase of actual stretching. The difference between the two kinds of ending may be summarised by saying that the secondary ending records simply the length of the muscle, while the primary ending records a combination of the instantaneous length of the muscle and the velocity at which it is being stretched. Functionally, this seems a fairly important difference but just how this different information is made use of by the central nervous system is not known. The velocity sensitivity of the primary ending makes it very sensitive to the high velocities produced in a muscle when it is vibrated. Both kinds of spindle ending stop discharging when the main muscle contracts; this is because the muscle spindles lie in parallel with the ordinary fibres and so are unloaded by contraction. In contrast, as already discussed, the tendon organs are excited by contraction.

The motor fibres to the muscle spindle are also of two functionally distinct kinds, and are called static fusimotor fibres and dynamic fusimotor fibres (fusimotor = motor to the spindle). It is probable that the functionally designated static fibres correspond to the histologically designated γ trail fibres, and that the dynamic fibres correspond to the γ plate fibres, but this is still not definitely established. The static fibres excite both the primary and the secondary afferent endings to discharge at a higher rate than before. This is because when the fusimotor fibres cause the intrafusal fibres to contract the poles of the intrafusal fibres extend their poorly striated central regions upon which the

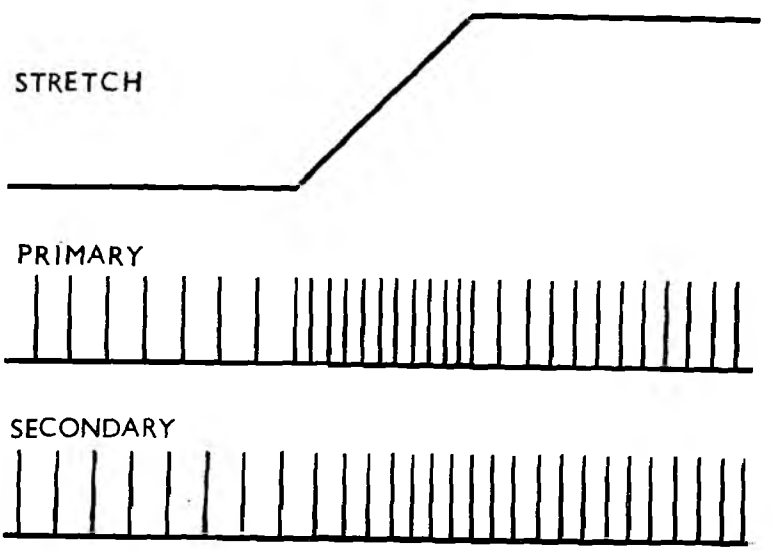

Fig. 4: The differing responses of the primary and of the secondary ending of a muscle spindle to a stretch of a muscle applied at constant velocity. The top trace shows the stretch applied to the muscle and is a graph of the length of the muscle against time; the total duration of the trace is 0.5 sec. The two lower traces show diagrammatically the nerve impulses which are set up by the two kinds of ending.

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 pre-synaptic 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