CHAPTER XI

Eye Movements. Stepping

EYE MOVEMENTS

Extrinsic Eye Muscles

Inasmuch as the extraocular muscles are controlled by their own receptors this regulation must ultimately subserve the needs of the organ of sight, that is fixation, vergence, scanning, pursuit movements and the automatic oscillations known as saccades, tremor and drift. Through fairly direct connexions of vestibular and neck receptors to their nuclei, the eye muscles take part in well known postural adjustments. There are no records of gamma-biased proprioceptive impulses from eye muscles actually engaged in any of these operations but against the background of present knowledge of spindle functions it is possible to make a number of sensible suggestions based on the information we possess about the properties of the gamma loop and spindles elsewhere.

The common laboratory animals, cat, dog and rabbit are without muscle spindles, defined as organs with capsules, nuclear bags, intrafusal fibres, motor endings and two kinds of sensory end organs in juxtaposition (Gilibar, 1910; Cooper & Daniel, 1949; Cooper & Fillenz, 1955). There are some muscle spindles in the eye muscles of the macaque, maximally six in each muscle (Greene & Jampel, 1966). But the extrinsic muscles of cats and rabbits are richly innervated with a variety of endings some of which must be sensory since their impulses reach the brain stem (Fillenz, 1955) and their impulses have been found to inhibit vestibular responses in the reticular formation (Gernandt, 1968). Single-fibre preparations of low-threshold stretch receptors and high-threshold tension receptors have been studied by Cooper & Fillenz in the cat and the monkey; the latter animal having a particularly large number of nerve fibres per muscle fibre in their extrinsic eye muscles. Bach-y-Rita with Murata (1964) and Ito (1966b) has extended the study of extraocular proprioceptors in the cat to a
systematic analysis of the properties of endings which pause in contraction and are thus of the "in parallel" type. They had many such receptors and also some of the "in series" pattern. Fundamentally in parallel behaviour need not be restricted to muscle spindles. It only requires the localization of the sensory end organ recorded from to be in a slower motor unit than the others contracting in response to the stimulus. In four cats the in parallel endings displayed a resting discharge in the slack muscle (the oblique inferior). Their threshold was of the order of 0.4 g at the minimum with peak values between 10–20 g in the distribution curve for the whole material. All of them responded by greater maximal firing rates to an increase of velocity of stretching and afterwards, with maintained stretch, displayed adaptation, the more so, the faster they had been firing. They differed from true spindles in continuing to run down in discharge rate as long as stretch was maintained. Afterwards, those with a resting discharge had not recovered within a 10 sec period of observation.

There were slowly and rapidly adapting spindle-like receptors in the cat's eye muscles but with regard to other properties all endings with a pause in contraction were essentially alike. This suggests that they are intimately dependent upon the properties of the muscle fibres themselves of which three types have been differentiated histochemically (Chap. I and for a review, Bach-y-Rita, 1970). Two main types have been described by functional studies, slow and fast, the former likely to be of two kinds, slow twitch fibres and true "tonus bundles" (Chap. I, p. 8, and Bach-y-Rita, 1959, 1970). In a recent review Peachey (1970) finds it likely that the eye muscles may contain five fibre types or as many as the Xenopus ileofibularis (Chap. I, Table 1). Zenker & Anzenbacher (1964) and Cooper (1966b) distinguish large and small fibres, the former authors describing them in considerable detail. The spindle-like receptors may well be the spirals surrounding the muscle fibres of extrinsic eye muscles, first described by Pallot (1934) and then by Cooper & Daniel (1949). The latter paper contains an excellent historical review of the literature on receptors in eye muscles. For later summaries, see Bach-y-Rita (1970) and Peachey (1970). Several good illustrations of tendon organs in extrinsic eye muscles were published already in 1890 by Ciaccio.

All this work has shown that eye muscles lacking spindles under fusimotor control nevertheless possess measuring instruments capable of recording length and tension. This raises interesting questions as to the reasons for the further developmental step leading to gamma-controlled muscle spindles in certain animals like man and the goat. Cooper & Daniel (1949) comment on this: "The voluntary movement of the eyes
as we know it in man is probably far from widespread in animals where
neck movements largely take place of extensive eye movements. A
macaque monkey will leap about with great skill, but each motion is
preceded by a quick turn of the head in the direction at which the
animal is aiming, or if it sits watching something its eye movements are
very small compared with the neck movements. It is in the higher
monkeys that eye movements are the most extensive, for sight is of the
greatest importance, the foveae are well developed, there is stereoscopic
vision, and the co-operation between the eyes and the forelimbs has
been enormously enhanced by the upright posture” (pp. 16–17).
Characteristically the cat also moves its head rather than its eyes in
surveying the visual field.

In the extrinsic eye muscles of man Daniel (1946) noted a structure
that looked like a spindle—at the time an unorthodox observation—
and Cooper & Daniel (1949) then started searching for spindles in eye
muscles. They saw them regularly in human material but always excludingly at the distal and proximal ends, never in the belly of the
muscle where they are found in the muscles of the extremities. The
smallest were 10 μ, the largest 50 μ in diameter. These spindles have
thin capsules and their intrafusal fibres are of about the same small
diameter as the surrounding extrafusal fibres (7–20 μ). Since they are
also short, from 50 μ to a little over 1 mm long, and surrounded by
nerve fibres and elastic tissue, it is easily understood why they escaped
notice for so long. Histologists (for example Cooper, Daniel & Whitter-
idge, 1955; Voss, 1957) have described two basic types of extrafusal
muscle fibres also in man, thin and thick, the latter forming a core
through the middle of the muscle. The simple spiral endings seem to be
restricted to the thick fibres (Cooper et al., 1955, in the goat).

In man there are about fifty spindles in each eye muscle, a figure of
the same order as holds for lumbricals. Tables giving number, dis-
tribution and some morphological features of spindles in the eye
muscles of man have been published by Merrilcees, Sunderland &
Hayhow (1950). Voss (1957) states that by his index (above p. 54)
the extrinsic eye muscles in man are among the spindle-richest in the
whole body. The largest number of spindles is found in the inferior
rectus suggesting, according to Cooper & Daniel (1949) an association
with the constant pre-occupation of the eyes with the hands. The tendon
organs are found at the ends of origin and insertion of the muscles.
Whitteridge (1955) has recorded from them in the goat.

This general description also fits goat and sheep, though Cooper et al.
(1951) report a larger number of spindles in sheep than in man, 120 in
the inferior oblique. For an enumeration of animals with and without
muscle spindles in the extrinsic eye muscles, see Cooper & Daniel (1949) and Bach-y-Rita (1959).

Cooper et al. (1951, 1954, 1955) have studied the discharges of single-fibre preparations and central nuclei as elicited from individual spindles in the extrinsic eye muscles of the decerebrate goat. As far as firing is concerned, the findings do not differ markedly from the ones reported for spindle properties in limb and intercostal muscles but so far there has been no separation of the effects of primaries and secondaries, dynamic and static fusimotor gamma fibres. However, to some extent it is possible to draw conclusions about fibre types from simultaneous stimulation of a number of gamma fibres. Thus in the intact eye-muscle preparation of the goat there is at light tension the characteristic irregular resting discharge (Cooper & Daniel, 1957) found by Eldred, Granit & Merton (1953) in hindleg spindles and shown in Fig. 27 Chap. III. This is held to indicate irregularities of spontaneous gamma activity. During stretching (Cooper & Daniel’s Fig. 5) the firing rate rose to about 300/sec and maintained an irregular activity below 100/sec. These values fell to about 140/sec and 10/sec respectively after cutting the motor supply while at the same time the firing rate became regular. Definite sensitivity to velocity of stretch is shown in their Fig. 1 and some records indicate so brief a pause after release of stretch (their Fig. 3b) that it seems reasonable to assume the presence of static gamma-fibre activity. The evidence of Whitteridge (1959) who stimulated branches of the IV nerve, which contained only gamma fibres, and found a large increase of position sensitivity (slope of impulse frequency-extension curve) seems conclusive on this point. As stated in Chap. IV this is a characteristic Type II effect of static fusimotor gamma fibres. The most striking effects of gamma stimulation in Whitteridge’s experiments were on the maintained discharge rather than on the velocity-sensitive component.

Functions of Eye Muscles

Too much attention need not be paid to the many reports of feeble or—mostly—absent stretch reflexes in the extrinsic eye muscles. As we have seen, muscle spindles in the limbs are very active in volitional contractions, yet normal subjects do not possess significant stretch reflexes. In the eye muscles, as elsewhere, they are likely to come into play when the alpha neurons are at or above their firing thresholds (Chap. VII), in accordance with the principle, repeatedly emphasized (above and Granit, 1968), that the gamma-supported stretch reflex is an adjunct to contraction. The missing link in this reasoning is the absence of precise anatomical information about the site of the pro-
jections of the spindle afferents. We have to assume them to be polysynaptic on the ocular motoneurons of the muscle from which they arise.

In vision the alpha motoneurons of the eye muscles have a number of special tasks to perform requiring high discharge rates. In man electromyographic recording from the small motor units of extrinsic eye muscles has shown firing rates of the order of 50–200/sec (Björk & Kugelberg, 1953), in cats and goats reflex responses at 140–170/sec have been noted (Reid, 1949). The muscles themselves (apparently their fast fibres) have been reported to respond with discrete contractions to tetanic oculomotor stimuli at 350–400/sec (Cooper & Eccles, 1930, with inferior rectus: Bach-y-Rita & Ito, 1966a). Motoneurons are unlikely to be able to discharge at such rates unless they have very high “gain”, as determined by the slopes of the spike frequency-current intensity curves of Chap. VI. They have short after-hyperpolarizations of the order of 40 msec (Eccles, Eccles & Lundberg, 1958), averaging 56 msec (Sasaki, 1963) and it has been impossible to demonstrate recurrent inhibition (Sasaki). Thus, once above their threshold for repetitive action, these motoneurons are likely to be unstable, as seen also in the records of Tokizane & Shimazu in Fig. 108 of Chap. VI illustrating stabilization of firing intervals in different muscles (including eye muscles). Bach-y-Rita & Ito’s (1966a) slow twitch fibres in the cat apparently deal with movements of a tonic type. The fast twitch has a rise time of 7 msec, the slow twitch one of 30 msec. The role of the true tonus bundles is unknown (Bach-y-Rita, 1967). The slow and fast phases of nystagmus in the cat, elicited by electrical vestibular stimulation, engage slow and fast muscle fibres respectively (Ito, Bach-y-Rita & Yamanaka, 1969).

It is apparent from the absence of spindles in the eye muscles of many animals that muscle length as such can be measured by simpler end organs, such as those in the cat. However, the spindle with its own motor supply is a far superior instrument of control. The genuine muscle spindles can maintain constant firing rates over long times and increase it by fusimotor action, very definitely static but apparently also dynamic. Controlled by the gamma loop, they have in their turn control over the central stations to which spindle afferents project. Spindle impulses from extrinsic eye muscles have been picked up in, for instance, cerebellar pathways, the eye muscle nuclei, the superior colliculus and the brain stem (Cooper et al., 1953a,b,c, 1955). The colliculus has a precise somatotopic projection of the retina, as first shown for the cat by Apter (1945) and then confirmed for other animals (see Whitteridge, 1960) Spindle secondaries have not yet been separated in eye muscle afferents.
Considering, to begin with, the eye movements in fixation, tremor is present also in an animal lacking muscle spindles such as the cat (Pritchard & Heron, 1960). It is of much the same amplitude in man and the cat. Basically it is thus independent of the type of proprioceptors present though the frequency is faster in man, 30–90 cycles/sec (Yarbus, 1967), up to 200 cycles/sec according to Ditchburn (1959) as against a maximum of 40 cycles/sec in the cat (Pritchard & Heron). The high fusion frequency of the eye muscles and the instability of firing of their motoneurons, mentioned above, are likely to provide a sufficient explanation of tremor. The irregular firing of the muscle spindles under gamma bias, pointed out by Cooper & Daniel (1957), may well contribute to the high tremor frequencies in man.

In the cat the small, involuntary “flicks” and saccades are rare events (Pritchard & Heron). In man they are a characteristic involuntary component in fixation and identical in the two eyes suggesting a common central site of issue. The saccadic movements have been studied by many authors for many years (see for example Yarbus, 1967 for a summary). Yarbus presents a graph of the distribution of the amplitudes of 1000 involuntary horizontal saccades. It shows a maximum between 2 and 13 min of angle. The duration of a saccadic movement is of the order of 10 to 20 msec for small ones below 1°; it may reach 60 to 70 msec for angles of 20°. If fusimotor neurons are to play a role for the large saccades, they would have to be precisely co-excited with the alphas. The anticipatory character of the dynamic response would be well suited for such fast operations. Cornsweet’s (1956) statement that saccades only depend on retinal cues for displacement is no argument against the interpretation of the role of the fusimotor fibres to be given below.

Saccades, as discussed above, have been defined as involuntary fast flicks of movement (see for example Yarbus, 1967, p. 103) in which both eyes move equally and simultaneously. They are, as stated, rare in the cat and possibly less common than in man also in the monkey which has very few muscle spindles (Greene & Jampel, 1966). Bizzi’s (1968) “voluntary saccades” in the unanaesthetized monkey are not what has been referred to in the previous paragraph. Bizzi’s finding of two types of neurons in the frontal eye field, one active in fast movements (his voluntary saccades), the other in slow pursuit movements, is of considerable interest. The different types of eye-muscle fibres suggest corresponding central elaborations of their neural control mechanisms (cf. Bach-y-Rita, 1970).

In the third type of involuntary eye movement in fixation, the so-called drifts, a retinal corrective reflex on the eye muscles would be fast
enough to be able to have gone round the collicular arc. Yarbus reports 300 msec as the most commonly found duration in man. The span of time is long enough to eliminate the need for a correction based on the automatism of gamma-activated spindles but this does not mean that spindle aid would be useless.

As is well known, it was shown independently by Riggs, Ratliff, Cornsweet & Cornsweet (1953) and by Ditchburn (1955) that the visual image tends to fade out if it is stabilized by elimination of the effect of the involuntary eye movements (cf. also Ditchburn, Fender & Mayne, 1959). This, in itself, is a perfect demonstration of the need for a meticulously controlled sensori-motor mechanism in vision. The retina evaluates and transmits the on-off variability obtained by such means. The gamma-controlled spindle seems ideally designed for improving this operation, especially when pushed to its very limit of speed and precision.

The systematic scanning of complex pictures, so well illustrated by Yarbus, is another instance of retinal co-operation with the motor apparatus in which voluntary and involuntary mechanisms of control play a part. It is open to doubt whether a relatively stationary animal (man as compared with bird) could build up a picture by scanning it in such detail as in Yarbus' illustrations without the support of controllable spindle sensitivity.

As our knowledge of spindle physiology has developed it has become evident that these sensori-motor end organs are automatic control instruments concerned with the adequate performance of our muscles. They do not measure force, position or what used to be called "Muskelempfindungen." Their cortical representation is insignificant compared with that of sense organs in the joints and in the skin. The eye muscles would be no exception to these rules. Brindley & Merton (1960) have found it impossible to detect passive movements of one eye or of both together after exclusion of visual cues and cocainization of the conjunctival sac. That no muscular end organs are concerned in the perception of the position of the eye ball.

The fast and precise integration of eye movements in compensation for postural adjustments of the head determined by the vestibular organs, the neck muscles, other tonic muscles and the cerebellum is one of Nature's wonders in the motor field. It has been much investigated in both the clinic and in physiological laboratories. Nystagmus is probably the most widely studied neural integration in the whole of neurology. Again the role of the muscle spindles in the extrinsic eye muscles has been neglected in this work, no doubt because it would be necessary to select an experimental animal which has these organs and
with all of them there are considerable technical difficulties to overcome. Eye movements other than nystagmus in response to vestibular stimulation have been repeatedly recorded by many workers, recently again by B. Cohen, Suzuki & Bender (1964) in the cat, by Azzena (1966) and Manni & Desole (1966) in the guinea pig, but without analysing their possible proprioceptive components. Cooper et al. (1953a,b,c) have pioneered in this field by reporting on short- and long-latency projections of eye muscle afferents to a number of central structures such as the vestibular nucleus, the superior colliculi and the centres for neck muscles, suggesting reflex proprioceptive control, and this at the moment is the limit of our knowledge. Inasmuch as muscle spindles are concerned, we can only assume, as was done above, that they would operate according to the rules discovered in analytically more accessible structures.

Possible Role of Proprioceptors in Eye Movements

The suggestion of Cooper & Daniel (1949) that the upright posture may necessitate spindle control of eye muscles cannot explain why these structures are found in ungulates such as the goat. This problem should perhaps be considered in relation to the decisive role of the neck muscles as governors of head movements (see below).

Like innervated leg muscles (Chap. VI last section) the extrinsic eye muscles generate total tension in proportion to extension. Collins, Scott & O’Meara (1969; cf. also Robinson, O’Meara, Scott & Collins, 1969) have found a proportionality constant of 5 g/mm in man and Fig. 119 illustrates a number of such curves at different initial lengths determined by positions of gaze of the unoperated eye. Assuming pure alpha control, parallelism of these curves seems improbable because under the circumstances mobilization of an increasing number of alpha motor-neurons is generally characterized by an increasing slope (Figs. 92 and 93). With striated muscles of the limb it is possible to produce a similar set of parallel curves by altering the amount of gamma activity (Fig. 91). These results suggest that also in the eye muscles some feedback mechanism is responsible for the parallelism of the curves of Fig. 119.

The explanation of such findings (following Matthews, 1959a, 1969) would be that they require co-operation of the tendon organs. The spindle discharge increases with increasing extension. Its excitatory component would therefore tend to increase the slope of the tension-extension curves at greater extensions. Since perfect linearity is being maintained over a great range of extensions, tendon organ inhibition is invoked to counteract excitation from the spindle primaries. Tendon
Fig. 119. Partially innervated length–tension curves for a human extraocular lateral rectus muscle. Change of muscle length from the primary position length is given in millimetres (first row) and its equivalent value in eye rotation (second row) if the radius of the eyeball is taken as 11.6 mm. Each curve is for a constant effort equated with the actual deviation of the unoperated eye temporal (T) or nasal (N) with respect to the eye under study. Curve PM is the passive muscle tension. Solid lines indicate the smoothed behaviour of total tension. Dashes are developed tension obtained by subtracting curve PM. (Robinson, O’Mera, Scott & Collins, J. appl. Physiol., 1969).

Organ inhibition is determined by total tension in contraction (Chap. V). To this reasoning might be added that present evidence shows the spindle secondaries to produce length-dependent inhibition in extensors (Chap. V). This factor may also be contributing to linearizing tension–extension curves. It is therefore suggested that the findings of Collins et al. should be explained by similar mechanisms of proprioceptive control. For muscle spindles to act under such circumstances it is necessary to assume fusimotor activity.

No sooner are these feedback mechanisms inserted into the governors of tension in extrinsic eye muscles than it follows as a corollary that they serve to maintain an approximate balance point of length at any given extension (setting of the gaze). The skeletal muscles do so by oscillating to an irregular fashion around the wanted length. The eye muscles with their extremely fast muscle fibres will oscillate at very much faster rates. Brief afterhyperpolarizations and lack of recurrent inhibition will contribute to the same effect. Furthermore, the fast motoneurons of ex-
trinastic eye muscles are likely to possess high gain. The results of Tokizane & Shimazu (Fig. 108) show their firing to be badly stabilized. Without spindles as misalignment detectors extraocular stretch reflexes based on other receptors could imitate these operations by a stretch-reflex feedback of simpler type but the addition of a gamma-loop adds versatility and precision to the process by making possible balanced control at any setting of gaze (length) demanded by the visual apparatus. Or, to put it differently, when it is maintained that eye movements are wholly controlled by a centrally “computed programme”, this may well be true, but this programme must be based on available “machinery” which includes the automatized operations of the gamma-loop.

We know too little about the relative tasks of slow and fast eye muscle fibres, their innervation, motor units and mechanical properties to be able to insert them into a picture of spindle control. The slow muscle fibres are likely to be employed in slow movements. There are, for instance, in man the slow vergence movements which Alpern & Wolter (1956) assume to be executed by slow muscle fibres. In the cat Yamana & Bach-y-Rita (1968) and Ito, Bach-y-Rita & Yamanaka (1969) have shown by intracellular studies that the steady tonic discharge of eye muscles is restricted to the slow fibres. These are also the ones which are active during slow spontaneous eye movements. Fast fibres were never seen to discharge in the absence of movement and but rarely in tonic movements. A comparison with conduction velocities in the abducens nerve during vestibular stimulation (electrical and by pressure) showed slow motor fibres (6–40 m/sec) to be active during the slow phase of nystagmus; the fast fibres (41–83 m/sec) appearing only towards the end of it. For further information, see the two papers referred to.

It is difficult to assess the role of load compensation in eye muscles provided with spindles as it would depend upon the relative amount of reciprocal and non-reciprocal activity in opposing extrinsic eye muscles. Assuming reciprocal activity dominant, there would only be a steadily increasing elastic force, originating in the orbital tissue, to counteract contraction in one member of a pair of opponent muscles. This force in man amounts to about 0.5 g/degree or 2.5 g/mm extension (Collins et al., 1969). It would be capable of producing a considerable increase of position sensitivity by resisting a contraction under static fusimotor control, assuming man to resemble the goat (Whitteridge, 1959) in this respect.

The co-operation of eye muscles with neck muscles in head movements is likely to involve the slow muscle fibres. With monkeys freely moving and allowed to climb Cohen (1961) has shown that cutting of
the insertion of the eye muscles plays a negligible role for head control. In contrast, anaesthetic blocking of the dorsal roots C1, C2 and C3 produces “severe defects in balance, orientation and motor coordination”. It was found by McCouch, Deering & Ling (1951) that the Magnus-de Kleijn reflexes are elicited by joints and ligaments in the first three cervical vertebrae. The contribution of the spindles was not considered in Cohen’s experiments, as removal of the information from proprioceptive afferents was total, nor did those of McCouch et al. exclude a contribution on the part of the spindles.

It was pointed out in Chap. II that the neck muscles are among the spindle-richest muscles in the body. These muscles undergo moderate changes of length but precise length-measuring must in this case be of great importance because localization and identification of objects by our two leading distance receptors in the head, the eye and the ear, would require extremely good regulation and maintenance of head position. From the point of view of motor control of muscle length by alpha–gamma linkage the neck muscles would seem to offer singularly interesting opportunities of study, also in relation to compensatory eye movements.

Vestibulospinal fibres make excitatory monosynaptic contact with many head extensor neck motoneurons in the C2–C3 segments (Wilson & Yoshida, 1969a). The relation between vestibulospinal fibres and neck motoneurons is therefore much closer, and less subject to local control, than the relation between vestibulospinal fibres and limb motoneurons.

Neck motoneurons can also be inhibited by fibres descending from the brain stem: these fibres originate in the medial vestibular nucleus, and the inhibition is monosynaptic (Wilson & Yoshida, 1969b). This demonstrates that the activity of some spinal motoneurons is subject to control by long inhibitory fibres descending from supraspinal levels. There is so far no indication of monosynaptic inhibition of vestibular origin in limb motoneurons, but recent results do show the presence of monosynaptic descending inhibition in thoracic motoneurons innervating back extensor muscles, and there is evidence that it is of vestibular origin (Wilson, Yoshida & Schor, unpublished observations).

The excitatory and inhibitory fibres originating in the vestibular nuclei and making synapses with neck motoneurons serve as relays for impulses originating in the labyrinth: electrical stimulation of the labyrinth evokes bilateral disynaptic excitatory and inhibitory potentials in neck motoneurons (Wilson & Yoshida, 1969c). The excitatory and inhibitory actions are presumably due to activation of labyrinthine afferents relaying in the lateral and medial nuclei respectively. These two direct pathways, acting reciprocally, provide the means for
accurate control of the neck musculature by labyrinthine receptors. The presence of such close coupling between the labyrinth and the motoneurons innervating the neck musculature is not surprising, because a prime role of the labyrinth is regulation of head position.

**STEPPING**

**Proprioceptors in Stepping**

Recent work on stepping suggests possibilities of analysing proprioceptive control and the role of the gamma loop in considerable detail. Stepping entails orderly activation of several limb muscles, beginning at the uppermost joint and ending with the foot, thus creating a sequence of complex changes of load and extension stimulating the muscle proprioceptors. There is also some knowledge of the interaction of limb muscle afferents at the spinal level which can be drawn on for explaining sequences and changes of phase in the step and, above all, the gait is a "natural" movement like respiration though evidently of far greater complexity and thus likely to reveal new aspects of proprioceptive control.

The old observation of Graham Brown (1911, 1914) that, fundamentally, walking movements are possible in spite of deafferentation of the limbs, should not be interpreted to mean that under such circumstances walking is identical in every respect with the normal gait. Nor is treadmill walking in the mesencephalic preparation, recently introduced by a group of Moscow workers (Severin, Shik & Orlovskij), perfectly normal, because as Lundberg (1969) has pointed out, fixation of the animal in a frame, as required for recording from root filaments, does not reproduce the normal effect of body weight on the muscles supporting stance. However, this work (Severin, Orlovskij & Shik, 1967a, b) is a pioneering attempt at sampling spindle and tendon organ impulses in dorsal rootlets and motor impulses in ventral roots (L7 of the cat) during walking and this, in itself, is worth the sacrifice of some other aspects of stepping.

In the experiments of Severin et al. stereotactic stimulation at 30/sec of the brain stem in a precolliecal cat induced walking whose rate was dependent on stimulus strength and the speed of the belt of the treadmill. In agreement with the concept of alpha–gamma linkage the discharge frequency of extensor spindle primaries at the ankle joint increased in the phase of stance, that of the flexors in the swing phase but the latter also fired when stretched by extensor contractions. The tendon organs were best activated during contractions of their own muscles. The spindle activity in the extensor did not in this case precede the
alpha activity, recorded electromyographically, but appeared in the phase of stance, afterwards lingering on for some time despite absence of alpha impulses. The co-activated fusimotor gamma fibres, very likely, were static fibres, because the spindles fired during muscle shortening. As described in Chaps VIII and X, dynamic and static fibres have generally been found to be simultaneously active despite definite evidence for basically independent control. Some dynamic fusimotor neurons may well have taken part in the linked alpha–gamma response of mesencephalic stepping. The participation of fusimotor gamma fibres has been demonstrated by Severin et al. (1967b).

From these results walking appears as a movement under strong proprioceptive control. The spindle secondaries have not been separately studied but static fusimotor activity is not likely to be restricted to influencing primaries. In the extensors these and the tendon organs would be inhibitory, the primaries excitatory, both these endings acting reciprocally on the antagonist. In the flexors the two spindle organs would cause autogenic excitation and antagonistic inhibition, the tendon organs autogenetic inhibition (Chap. V). The information to higher centres would concern length and tension but in the motor field of study "information" tends to be but modestly informative unless it can be shown precisely for what particular motor act it is of importance. Knowledge of this kind is restricted to motoneurons, whose net depolarizing pressure is an algebraical sum of plus and minus terms (Chap. VI). In considering the role of muscle spindles in stepping it has previously seemed natural to think of them as stretch receptors acting in response to passive stretch only. Clearly alpha–gamma linkage in locomotion, in analogy with its role in postural reflexes and respiration, should be thought of mainly as a mechanism making use of stretch reflexes during active contractions. In the flexors—at least those recorded from—the spindles act in contractions as well as in passive stretch. An interpretation will be given below.

By recording from cut ventral roots in the lumbar region the rhythmic motor activity induced by mesencephalic stimulation was followed in fourteen animals which then were curarized by Flaxedil (Shik, Orlovsjik & Severin, 1966). In this preparation the rhythmic activity disappeared when all the limbs became slack but when the limb represented in the root recorded from was moved in imitation of a step, distinct rhythmic activity reappeared, provided that this was done during mesencephalic stimulation. Passive limb movement did not by itself suffice to elicit this effect. Normally, in mesencephalic stepping, deafferented hindlimbs move with the forelimbs, albeit after some delay, but stop moving when the forelimbs are held fast.
The complexity of the central organization of stepping is well illustrated by these two experiments, which demonstrate the importance of the proprioceptive input acting in combination with central drive as well as by long spinal reflexes in co-operation with the centres for the two pairs of limbs.

Unrestrained Walking

The work of Engberg & Lundberg (1962) and of Engberg (1964) together with some as yet unpublished results, all on walking in the unrestrained cat, has recently been reviewed by Lundberg (1969) in a discussion of reflex stepping including also some of the historical background in this field. A major aim of this work has been to incorporate into our knowledge of proprioceptive control the distribution of afferent projections from the sense organs to the different motor nuclei engaged in the act of stepping.

Dominance of central control makes the extensors initiate their activity some 5–10 msec before the foot touches the ground. This is, as it were, an anticipating operation on the “central programme” and independent of the position of the other limbs as well as of stretch reflexes. Lundberg’s assumption is that this programme starts a simple reciprocal alternation between flexor and extensor excitation and inhibition (cf. Shik et al., 1966). Accordingly he sets himself the task of finding out to what extent it is possible to explain the differential activation of the various muscles along the limb by proprioceptive reflexes. The phase of swing begins with flexion in which the hip movement carries the limb forward while in its later phase knee extension occurs to produce the stride. All extensors are active in the stance in spite of which there occurs a temporary flexion of knee and ankle in the middle of the phase of stance owing to the limb yielding under the weight of the body. Hip extension is maintained throughout stance. Yielding is more prominent in the gallop than in walking.

It is surprising that yielding, which is an important feature of the normal gait, occurs in the very muscles proved in the previous section to be governed by alpha–gamma linkage. (Very likely linkage is general but there is no direct evidence for hip extensors.) It means that load compensation is temporarily overcome, probably by an inhibitory force. This inhibition could come from (i) the tendon organs in the contracting extensors; (ii) from spindle secondaries co-activated with primaries in static fusimotor action or be (iii) centrally determined (if one refuses to accept Lundberg’s very reasonable basic assumption). His most important argument favours inhibition from the tendon
organs because their afferent projections interconnect knee, ankle and foot extensors in the spinal cord (Eccles et al., 1957b; R. M. Eccles & Lundberg, 1959a). On the whole, however, load compensation must be important in the phase of stance which carries the body weight in both walking and running, uphill and downhill, these acts obviously involving great variations of load.

Another interesting point is the maintained spindle discharge of the flexors (Severin et al., 1967a) when they are stretched by passive extension. This discharge will act in a double way. It will antagonize extensor contractions by reciprocal inhibition from spindle primaries and, if strong enough, maintain a slight flexor contraction similarly—and probably more powerfully—antagonizing the extensors. It seems essential for smooth performance that muscles should contract against some inhibitory restraining influence. It is as if the net depolarization of a motoneuron required the minus terms for perfect control in gradation of firing rate. We know that inhibition will hold the discharge to its primary range with algebraical summation as a consequence.

The leading hip extensor (adductor femoris) receives spinal projections of spindle primaries also from the knee extensors (R. M. Eccles & Lundberg, 1958b) and so can benefit from the alpha–gamma linkage of these muscles in the phase of stance when a high degree of load compensation is required, for example as in walking uphill. Lundberg (1969) points out that the hip extensors are important in propulsion of the body and suggests that this function requires the high safety factor entailed in this extensive overlap of the spindle projections in the spinal cord.

The distribution of spindle and tendon organ projections between the individual motor nuclei of the spinal cord would seem to be of special interest for the interpretation of the role of the double-joint muscles whose action will be dependent upon a sequence of movements partly of their own shaping. An example: a double-joint flexor of the hip (for example the lateral sartorius) also produces extension at the knee. To begin with, the knee flexors, activated on the general “flexor programme” are strong enough to prevent extension but, as flexion proceeds, it will in the end stretch the double-joint muscle which, operating on alpha–gamma linkage, will respond with an intense barrage of spindle impulses. In addition to exciting the hip flexor motoneurons these impulses also produce reciprocal inhibition on those belonging to knee flexors. Thus, as the swing evolves, the knee flexors, excited on the “general programme”, will in the end suffer inhibition from the spindles of the double-joint muscle and by this means contribute to the differentiation of the central programme into co-ordinate stepping.
These examples should suffice to illustrate the idea of a proprioceptive elaboration of a relatively simple central command alternating between flexors and extensors. There are still many missing facts, the secondaries are, for instance, left outside Lundberg’s picture and the knowledge of the distribution of the proprioceptive projections is based on a restricted number of single cells, but it is definitely an approach which deserves to be followed up, if for no other reasons, because it shows spindle action inserted into a complex muscular act and tries to understand the role of the proprioceptors in stepping (cf. also Chap. V, p. 120).