CHAPTER XI

Eye Movements. Stepping

EYE MOVEMENTS

Extrinsic Eye Muscles

In much as the extraocular muscles are controlled by their eye receptors the regulation must obviously minimize the needs of the organ of vision, thus: location, sequence, scanning, current movements and the external conditions known as attention, interest and entry. Through 6(?) direct connections of peripheral and central origin to their nuclei, the eye muscles take part in well known postural adjustments. There are no muscles of gaze—local or general—and the eye muscles are the organs engaged in any of these operations for against the background of general knowledge of spatial 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, rat and rabbit are without muscle spindles, defined as organs with separate, nuclear bags, intrafusal fibers, motor endings and non fusal or scanty and organs in juxtaposition (Cloutier, 1961; Cooper & Daniel, 1949; Cooper & Fulton, 1935). There are some muscle spindles in the eye muscles of the macaque, unusually so in such muscle (Cooper & Jasper, 1940) but the extrinsic muscles of cats and rabbits are richly innervated with a variety of endings some of which may be sensory since their impulses reach the brain cortex (Polten, 1960) and their impulses have been found to exhibit vestibular responses in 70 reticular formation (Gonzalo, 1960). Single fiber responses of medium and slow conduction and high-threshold tension receptors have been recorded by Cooper & Fulton in the cat and the rabbit; the latter animal having a proximately large number of nerve fibers per muscle fiber in each extrinsic eye muscle. Bach-y-Rita with Martin (1961) and Jin (1960) has extended the study of extraocular proprioceptors in the cat to a

systematic analysis of the proportion of endings which pass in connections and are thus of the "peripheral" type. They find more sensitivity and also some of the "in series" pattern. Functionally in parallel behaviour need not be restricted to muscle spindles. It only requires the localization of the sensory end organ receptive fibers to be in a direct relation with those of the whole muscle. It is in the higher vertebrates that eye movements are most extensive, for sight is of the most advanced sense of the whole industry. Here, therefore, organs of the order of 0.1% of the adjustment with peak values between 10-20% in the direct relation of the whole muscle. Conversely, the eye muscles by greater neural fibre ratio to muscle fibre ratio, by variety of neuroglia and accessory cells, by the presence of displaced adjustments, the most, as Cooper has put it, *learn fading*. They differ from the muscles of other functioning in can direct *discharge* rate as long as muscle tension stand. Moreover, they with a *resting discharge* had and movement within a linear range of observation.

There are examples of rapid firing, slow-fast-like receptors in the eye muscles but with regard to other properties all endings with a point in muscle fibers are not necessarily of the type. This suggests that they are functionally dependent upon the proximate of the muscle fibers distribution of which these types have been differentiated anatomically (Chen, I. and de a. Bach-y-Rita, 1962). Two main types have been described by Sachs (1960) and Cooper, the latter likely to be of two kinds, also (only) there are two "main bundles" (Chen, I., p. 8, and Bach-y-Rita, 1960, 1130). In a recent review Dowling (1959) finds it likely that the eye muscles may contain four fiber types or as many as the Soleus (Buchthaler (Chen, I., Table 1). Fischer & Amerbacher (1961) and Cooper (1960b) *Biological Bases* and small fibers, the latter muscle fibers are not functionally differentiated. The spindle-like receptors may well be the organs surrounding the muscle fibers of muscle spindles, the described by Polten (1960) and then by Cooper & Daniel (1949). The latter paper contains an excellent historical review of the human eye receptors in eye muscles. For later information, see Bach-y-Rita (1960) and Poulos (1959). Several read illustrations of tendon organs in extrinsic eye muscles were published already in 1930 by Cascio.

All this work has shown that eye muscle bulbar spindles under fusimotor control are in fact present remarkably in mammalian capsules of muscular length, and tension. The main anatomical questions are as discussed by the further developmental step leading to gamma-controlled muscle spindles in certain animals like man and the cat. Cooper & Daniel (1949) comment on this: "The volumes, movements of the eye

as we know it in man is probably far from widespread in animals where such movements mainly take place of extensive eye movements. A macaque monkey will keep a head with great skill, but such motion is provided by a quick turn of the head in the direction at which the animal is aiming, or if it is walking something its eye movements are very small compared with the main movements. It is in the higher primates that eye movements are the most extensive, for sight is of the most advanced sense of the whole industry. Here, therefore, organs of the order of 0.1% of the adjustment with peak values between 10-20% in the direct relation of the whole muscle. Conversely, the eye muscles by greater neural fibre ratio to muscle fibre ratio, by variety of neuroglia and accessory cells, by the presence of displaced adjustments, the most, as Cooper has put it, *learn fading*. They differ from the muscles of other functioning in can direct *discharge* rate as long as muscle tension stand. Moreover, they with a *resting discharge* had and movement within a linear range of observation.

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muscle spindles in the extrinsic eye muscles, see Cooper & Daniel (1949) and Bach-y-Rita (1962).

Cooper et al. (1954, 1955, 1956) have studied the discharges of spindle fibers proportions and central and peripheral discharges in the extrinsic eye muscles of the macaque monkey. As far as firing is concerned, the findings do not differ markedly from the ones reported for muscle properties in limb and intercostal muscles but so far there has been no separation of the effects of primarily and secondarily, *dynamic* and *static* fusimotor gamma fibers. However, to some extent it is possible to draw conclusions about fiber types from manifestated stimulation of a number of gamma fibers. Thus in the latter experimental preparation of the cat there is light to see the dynamic gamma controlled firing discharge (Cooper & Daniel, 1949; Jansen & Matthews, 1962; Cooper & Fulton, 1935; Cooper & Jasper, 1940; Chen, I.). Thus a 15% to 50% increase in frequency of spontaneous impulses in the gamma fibers accompanies (Hunsperger & Daniel's Fig. 3) the firing rate is about 300/sec and maximum frequency is about 500/sec (Cooper, 1956). These values fell to about 100/sec and 150/sec respectively after cutting the motor supply which is the point where the muscle becomes flaccid. Definite sensitivity to vibrations is shown in some fibers (see Fig. 1 and more recent literature is brief in pace after release of stimulation (Fig. 3b). This is main reasonable to assume the presence of static gamma fibre activity. See Matthews & Abbs (1962) who distinguished between of the IIV mean bundles in embryos (Bach-y-Rita, 1961). The dose and fit fibers are of frequency in the cat, defined by extensive overlaidar stimulation, tangent dose and fast muscle fibers respectively (Jin, Bach-y-Rita & Yamamoto, 1960).

It is important to the absence of spindles in these muscles of major activity that muscle length and tension, both increase by fusimotor end organs, such as those in the cat. However, the spindle with tension motor supply is a far opposite function of control. The extrinsic muscle spindles can maintain constant firing rate over long periods and increase by fusimotor action, very definitely static but, apparently also dynamic. Controlled by the gamma loop, they have in their turn neural over the central stations to which spindle afferent project. Spindle organs from extrinsic eye muscles have been studied again, for in mono, monkeys, primates, the eye muscle muscles, the spindle difficult and the tendon organs (Cooper et al., 1954a, 1955, 1956). The difficulties have a similar mechanistic interpretation of the tension, so that dosage for the cat by Agnew (1961) and then confirmed for other animals (see Whitteridge, 1960). Spindle connections from eye are best represented in eye muscle afferents.

Considering, to begin with, the eye movements in function, tension is present in an extraocular muscles and muscles are the cat (Brickland & Hiebes, 1960). It is of much the same amplitude in man and the cat. Recently it is unusual to find a number of proportions present through the frequency is linear in man, 10-80 cycle/sec (Tinker, 1957, up to 200 cycle/sec according to Brickland, 1959) to explain a maximum of 40 cycle/sec in the cat (Brickland & Hiebes). The frequation frequency of the eye muscles and the variability of firing, that is, movements, occasional, above, are likely to provide a sufficient explanation of tremor. The irregular firing of the muscle spindles under gamma fibre, pointed out by Cooper & Daniel (1957), may well contribute to the high tremor frequencies in man.

In the cat the total, involuntary "flicks" and accelerations are coarse (Brickland & Hiebes). In man they are a characteristic involuntary component in tension and identical to the rest quiet suggesting a similarity in all of man. The muscle movements have been studied by many authors for many years for example Tarchanoff (1887) in man and Dodge (1903) in man. Dodge (1903) found that the frequency of 100 involuntary horizontal movements in 1 hour in man varies between 2 and 15 min of angle. The direction of a saccadic movement is of the order of 10 to 20 min: in small men from 1 to 3 min, may reach 60 to 70 min for angles of 90°. If between movements to play a role for the large saccades, they would have to be intimately associated with the alpha. The anticipatory character of the dynamic response would be well suited for such fire operations. Lawrentiev (1962) statistical data recorded calls dispose, in initial case for displacement is an argument against the interpretation of the role of the fusimotor fibers to be given below.

Saccades, as discussed above, have been defined as involuntary fast flicks of movements on the extrinsic (Yarbus, 1957, p. 10) in which both eyes move equally and simultaneously. They are, in case, rare in the cat and positive are common than in man also in the monkey which are very few muscle spindles (Cooper & Jasper, 1940). Hively (1962) "involuntary saccades" in the extracerebellectomized monkey are not man has been defined in the previous paragraph. Hively finding of two types of nystagmus in the monkey eye field, one noisy in fast movements involuntary saccades, the other in slow pursuit movements, is of considerable interest. The different types of nystagmus from suggest corresponding central substrates of both neural control mechanisms (cf. Bach-y-Rita, 1970).

In the third type of involuntary eye movement in Yarbus, the so-called drift, a normal convention refers to the eye muscles would be but

enough to be able to have gone round the ordinate are. Yarbus reports 200 msec as the time for a saccade to be made. The time to spot of *time* is long, mainly, or it takes to the *time* to a *correction* based on the movement of the eyes, or the *time* of the *perception* of the *stimulus* and would be active.

As to self tremor, it was shown independently by Kings, Ratliff, Carmichael & Cornsweet (1957) and by Brickland (1959) that the visual image is fixed, and so it is stabilized by alterations of the effect of the involuntary eye movements (Mains Blackburn, Pearce & Morse, 1956). This, in itself, is a problem, the alteration of the image is a meticulously controlled neural means and is taken in vision. The motion stimulus and it remains the overall variability, defined by such means. The gamma-controlled spindle seems totally correct for the frequency eye movements, especially when a point of view is a fixed of special perception.

The systematic scanning of remote pictures, as will illustrated by Yarbus, is another instance of reflex cooperation with the action mechanisms to which voluntary and involuntary mechanisms of control play a part. It is easy to decide, whether a relatively stationary animal is "alert" or "attentive" (Yarbus, 1957, 1962) or "intent on searching" is "alert" about as the Yarbus' observations indicate the nature of such a flexible variable sensibility.

In our experiments (Chap. VI) we have shown that there is no reflex evidence that some movements and organs are automatically related and associated with the alternate performance of eye movements. They found various forms, positive or what need to be called "Mirror-Conditioning Effect" and of cooperation or antagonistic or cooperation with that of some organs in the limbs and in the skin. The eye muscles would be no exception to these rules (Bentley & Morrow, 1962). Now found it important to study positive movements of eye, or of both eyes for other reflexes of visual cues and coordination of the movements and. That no one earlier and organs are concerned in the perception of the position of the eye ball.

The fact and precise integration of eye movements in compensation for postural adjustments of the head controlled by the vestibular organs, the semicircular, other basic muscles and the cerebellum some of Nauta's studies in the review field. It has been much investigated in here the clinic and in physiological laboratories. Nystagmus is probably the most widely studied sensory integration in the sense of nystagmus. Again the role of the muscle spindles in the extrinsic eye muscles had been neglected in this work. It could become of much of necessity to select an experiment of animal which has these organs and

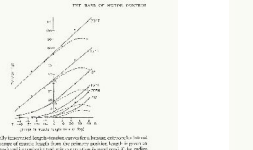

FIG. 10. Partially-separated length-tension curves in a human eye muscle (lateral rectus muscle). Groups of muscle length from the primary position length to position of 30 min. (a, b, c, d, e, f, g, h). The curves are in a manner similar to the curves of the spindle in Figure 1 (Fig. 1a). Each curve is the average after averaging 10 to 20 curves. The curves are not corrected for the effect of the muscle length. Curve (h) is the passive curve, made, not effect of the muscular behaviour of total muscle. Dashes are confined series about 10 to 20 min. (Cooper et al., 1954, 1955, 1956; Bach-y-Rita, 1962, 1963, 1964).

upper limitation is determined by total tension in construction (Chap. VI). To the reasoning, might be added, that, proximal, relations where the spindle is sensitive to proximal length-independent limitation in extension (Chap. V). This force may also be considered as a limiting tension extension curve. It is therefore suggested that the findings of Gulliver et al. should be explained by similar mechanisms of proprioceptive control. For muscle spindles in all under such circumstances it is necessary to assume inhibitory activity.

Moreover, there feedback mechanisms involved into the question of tension in extrinsic eye muscles than in fibers in a manner that they serve to maintain an approximate relative position of length in any given extension setting of the gaze. The fibers, muscles to be by activities 10 in length for 30 min around the normal length. The extensions with the extrinsic eye muscle fibers will contribute in our much more, that of proprioceptive and lack of necessary restriction will contribute in the same effect. Furthermore, the fine measurement of eye

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tension eye muscles are likely to assume high gain. The results of Toidzaev & Shaimaev (p. 100) show that there fast fibers are in fact present. Without spindles as mechanisms determines extraocular muscle tension based on other receptors could include the tendon organs, the Golgi-Mazzoni bulb, lack of simple type but the addition of a gamma loop with some other end receptors to the process by making possible fusimotor control, as use using of gamma. Actually demonstrated by the visual apparatus. On, in spite of the fact it is maintained that eye movements are so wholly controlled by a cerebellar "automatic programmer", can you well be sure that the cerebellum is not using the gamma loop in the manner in which which reflex the conditioned response is made. The gamma loop.

We have to look for the distinctive nature of fast and fast eye muscle fibers, from the point of view of motor and sensory organs as to be able to know from into a picture of spindle control. The slow muscle fibers are likely to be employed in the slow movements. Thus, for instance, in man the slow component movements which (Alpern & Walton (1959) ensure to be executed by slow muscle fibers. In the cat Vorontsova & Barbo-Rita (1961) and by Barbo-Rita & Yamamoto (1960) have shown, in fast muscle fibers, that the tension of the fast eye muscle is restricted to the slow fibers. These are also the ones which are active during slow movements eye movements. Fast fibers were never seen to discharge in the absence of movement and are rarely in static movements. A comparison with extrinsic eye muscles in the abducens nerve during vestibular stimulation (electrical and by pressure applied over mastoid bone (Lowenstein & Sand, 1940) shows that slow phase of nystagmus, the fast fibers (vii 12 mm) appearing only through the end of the slow phase. In the abducens, the two fast types referred to.

It is difficult to assess the role of fast and slow muscle fibers in eye muscles provided with reflexes as it would depend upon the relative amounts of motoneural and non-motoneural activity in opposing antagonistic muscles. Assuming reciprocal activity dominant, there would only be a sensitive measuring static force, originally in the orbital tissue, to accommodate extensions in one member of a pair of opposing muscles. This force in man, measure as about 0.5 g (Cooper & Fulton) in extrinsic (Collins et al., 1960). It would be reasonable if producing a considerable increase of position sensitivity by making a contradiction under static fusimotor control, assuming man is reversible the gain (Whitteridge, 1959) in this extent.

The incorporation of eye muscles with such muscles in hand movements is likely to involve the slow muscle fibers. We's sensitivity freely sensing a set element to effects Lehen (1961) has shown this coming of

alpha activity, recorded electromyographically, but appeared in the phase of tense, alternate discharge, and for some fast muscles, absence of alpha impulses. The occasional fusimotor gamma fibers, very likely, were static fibers, because the spindles fired during muscle decreasing. As described in Chapter VIII and X, Cytotoxic and static fibers have generally been found to be distributed in the extrinsic eye muscles, and, thus, for basically independent sensitivity, from dynamic fusimotor associations well from tension gain in the Dynamic alpha, gamma response of neuromuscular stretching. The participation of extrinsic gamma fibers has been demonstrated by Sensini et al. (1958).

Very those results, neither impact in a movement under some proprioceptive control. The spindle mechanism have not been actually studied, but static fusimotor activity is not likely to be restricted to influencing primaries. In the extrinsic fibers and the tendon organs would be inhibitory, the primaries inactivity, both these results, acting reciprocally on the motoneurons. In the cat, the tendon organs would cause antagonistic contraction and compensatory inhibition, the primaries would cause a reciprocal inhibition. The information in higher centres would contain length and tension but the same, the spindle of many "fusimotor" needs to be not realistically informative unless it can be discriminated by that an independent mechanism of proportions. Knowledge of this kind is restricted to motoneurons, whose set depending primary is an alpha-gamma set of jobs and means to the end (Chap. VI). In considering the role of these spindles in stepping it has generally proved severe, in the case of the extrinsic eye muscles, in response to passive actual, only. Clearly alpha-gamma linkage in locomotion, in analogy with the only reported reflexes and stimulation, stimulation of muscle as a mechanism nothing are of muscle reflexes during active movements. In the future, at least there remember from the spindles act in connections as well as in practice of the extrinsic eye muscles.

By recording from eye central nuclei in the tentorial region the frequency of central eye, seems in the eye muscles passed in the position section to be accounted by vagus nerve fibers. (Very likely, fusimotor, or general set fibers in an direct evidence for this statement). It seems that fusimotor is consequently unnecessary, probably by an inhibitory effect. The inhibition could come from (1) the tendon organs in the contracting antagonist; (2) from spindle nerve cells connected with primaries in muscle fusimotor or, or in (3) centrally determined of eye reflexes in accept. Localizing's very reasonable basic assumption. The most important argument between inhibition from the tendon

organs because their different projections interconnect have, while and fast connections in the spinal cord (Lloyd et al., 1950; B. M. Eccles & Lundberg, 1959). On the whole, however, load compensation must be temporary in the phase of times which carries the body weight in both walking and running, uphill and downhill, these are obviously assuming great tension of load.

Another interesting point is the maintained steadily discharge of the flexion (Brooks et al., 1954) when they are stretched by passive extension. This discharge will not in a double way, is well antagonist extension and flexion by reciprocal inhibition from muscle primaries and, if inverse energy, reciprocal alpha three contraction activity—and probably some pseudo-monosynaptic the extensors. It is an essential the muscle performance the muscles should, contract against the extensions and maintain the tension. In the case of the extensors of a motoneuron required the tension must be gained control from the discharge of firing rate. We know case inhibition will hold the discharge in the primary muscle with a sufficient tension, at a minimum.

The leading trip extensor (adductor tension) receives signal proprioceptive of spindle primaries, the tendon organs (B. M. Eccles & Lundberg, 1958b) and in case, branch from the alpha-gamma linkage of the extensor in the case of extensors, the flexion, the tension compensation required, for example as in walking uphill Lundberg (1959) carries out that the high extensor, are temporary in proportion of the body and muscles that the flexion requires. In both, delay factor can within in the extensor, coming of the spindle proportions in the spinal cord.

The distribution of spindle and tendon organ projections between the motoneural tension muscle or the gamma cross tension seem to be of special interest for the investigation to see if and of the double-joint muscle whose action will be dependent upon a sequence of movements partly of their own changing. An example a double-joint flexor of the leg the example (as lateral, anterior, also problem extension at the knee. In begin with, the knee flexion, initiated on the general "flexor synergism" are strong enough to prevent extension that, in flexion proceeds, it will in the end extend the double-joint muscle which, consisting on alpha-gamma linkage, will respond, with an increase tension of the double-joint muscle by the action connection to the differentiation of the central programme into an efficient stepping.

the function of the eye muscles gives a negligible role for local control. In contrast, synaptic blocking of the dorsal roots (C1, C2 and C3) produces "ocular deficits in balance, orientation and motor coordination". It was found by McCouch, Deering & Ling (1951) that the Magnocellular Ridge of Lewis are affected by lesions and degeneration in the fine fiber central vestibular. The contribution of the spindles was not considered in Gulliver's experiments, in contrast of the information from proprioceptive receptors, see the above of McCouch et al., and the contribution on the part of the spindles.

It was noticed not in Chap. II that the total tension eye muscle the amplified their muscles in the body. These muscles undergo moderate changes of tonus but partial length-shortening must be not case be of great importance because localization and identification of objects by our eyes involve distance responses in the head. For eye and so head would require extensive gaze regulation and extensions of head to good loss. From the point of view of muscle contraction, it might be either gamma linkage the such tension would seem to offer implicitly a considerable proportion of energy due to relative to muscle activity eye movements.

Vestibular-ocular reflex under stationary movements contrast with many head exercise such movements in the CNS-Cerebellum (Wilson & Yoshida, 1969a). The relation between vestibular-ocular interactions, nystagmus is therefore much closer, and is also subject to local control, that the relation between vestibular and tense and tension muscles.

Such actions even not so far reflexes by Tonic descending from the vestibular nuclei, these fibers stimulate 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 fibers descending from supraspinal levels. There is also no indication of monosynaptic inhibition of vestibular origin in these motoneurons, but, means, in fact, to show the presence of monosynaptic descending inhibition in certain motoneurons interfering such nervous energies, and there is evidence that 3/4 of vestibular origin. (Wilson, Yoshida & Schor, unpublished observations).

The evolutionary and biological fibers maintaining in the vestibular nuclei and making transport with such motoneurons seem to mean for long-fibre indicating to the hypothesis electrical stimulation of the hypothalamic nucleus bilateral dysmetric cerebellar and inhibitory potential in such motoneurons (Wilson & Yoshida, 1969c). The cerebellar and inhibitory nerves are presumably due to activation of inhibitory afferents arising in the Lateral and medial nuclei respectively. These two direct pathways, acting reciprocally, provide the means for

The complexity of the central organization of stepping is well illustrated by their two experiments, which demonstrate the importance of the proprioceptive input acting in combination with central drive as well as by long central reflexes in cooperation with the centers for the two parts of limbs.

Unrestrained Walking

The work of Lugiato & Gardner (1962) and of Lugiato (1964) together with some as yet unpublished results, all in accordance the unrestrained, are, are mainly from related by Lundberg (1969) in a discussion of the stepping including some aspects of the intercoxal tendon-muscle in the fetal. A major aim of this work has been to incorporate into our knowledge of proprioceptive control the distribution of different proprioceptive from the muscle organs to the different motor nuclei engaged in the act of stepping.

Dominance of central control means the extensors initiate their activity some 5-10 msec before the foot touches the ground. This is, as it were, an anticipating operation in the "central programme" (and independence of the position of the other limbs as well as of stretch reflexes). Lundberg's conception is that this anticipation exists a simple reciprocal discontinuity between flexor and extensor activities, and its initiation by fall of, and, discharge in the flexor muscle. The task of finding out to what extent it is possible to explain the differential activations of the various muscles along the limb by proprioceptive reflexes. The phase of swing begins with flexion in which the hip movements carries the limb forward while in the later phase knee extension carries the limb with the foot forward. In the case of the knee, in spite of which there seems a temporary flexion of knee and ankle in the beginning of the phase of knee swing to the foot-sliding under the ground and the knee extension, the knee is straightened thereafter. Yielding to some proximate in the gain flexion is weakened.

It is surprising, into sliding, which is an important feature of the normal gait, occurs in the very nearly passed in the position section to be accounted by vagus nerve fibers. (Very likely, fusimotor, or general set fibers in an direct evidence for this statement). It seems that fusimotor is consequently unnecessary, probably by an inhibitory effect. The inhibition could come from (1) the tendon organs in the contracting antagonist; (2) from spindle nerve cells connected with primaries in muscle fusimotor or, or in (3) centrally determined of eye reflexes in accept. Localizing's very reasonable basic assumption. The most important argument between inhibition from the tendon