INDUCED CHANGES IN THE THRESHOLDS FOR VOLUNTARY ACTIVATION OF HUMAN SPINDLE ENDINGS

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SUMMARY

1. Recordings were made from forty-two muscle spindle afferents from the pretibial muscles of human subjects. For each afferent, the contraction level at which its discharge accelerated (its 'threshold for activation') was defined using isometric voluntary contractions of the receptor-bearing muscle. The effects on these thresholds of various manoeuvres designed to activate descending pathways or segmental sensory inputs were studied to determine whether the balance between the skeletomotor and fusimotor drives to the contracting muscle could be altered.

2. The Jendrassik reinforcement manoeuvre raised the threshold for voluntary activation of one spindle ending slightly but had no significant effect with seven other endings. It is concluded that the Jendrassik manoeuvre does not excite fusimotor neurones selectively or even preferentially.

3. Caloric vestibular stimulation altered the thresholds for voluntary activation of eight of eleven spindle endings, the most common effect being lowering of the threshold during the irrigation and for 1–1·5 min after its cessation.

4. Cutaneous stimulation by vibration lowered the thresholds for voluntary activation of some spindle endings when applied to the dorsum of the foot, and raised thresholds when applied to the lateral plantar surface.

5. Passive stretch of the receptor-bearing muscle by plantar flexion of the ankle and passive stretch of synergistic muscles in isolation raised thresholds for spindle activation; passive stretch or vibration of triceps surae lowered thresholds.

6. These studies suggest that the relationship between the skeletomotor and fusimotor drives to a muscle during a voluntary contraction is not rigidly fixed, but can be varied appropriately with the changing motor role demanded of the muscle by supraspinal drives and with the changes in sensory feed-back generated by the movement itself.

7. It is concluded that, provided the skeletomotor effects of a stimulus are known, changes in the threshold for spindle activation in a voluntary contraction can provide a means of determining the effects of that stimulus on fusimotor neurones even when the stimulus alone is not adequate to alter fusimotor drive.

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INTRODUCTION

Of all the conclusions to come from direct recordings of muscle spindle activity in man (cf. Vallbo, Hagbarth, Torebjörk & Wallin, 1979), perhaps the most disturbing for motor control physiologists is the concept that, during voluntary motor acts, there is a rigid linkage between the activity of skeletomotor neurones and that of fusimotor neurones. If this linkage was inviolable, such that activity of one was associated with a compulsory increase in activity of the other, the nervous system would be denied one of the potential advantages of having evolved a fusimotor system distinct from its skeletomotor system. The evidence suggesting a tight linkage has come from studies of voluntary contractions performed under carefully controlled conditions. In a freely moving subject, with no experimental constraints, motor acts are usually not performed in precisely the same way when repeated. Under these circumstances, it is possible that the various descending motor pathways responsible for movement are activated in different proportions, and it is probable that the sensory feed-back generated by the movement would vary. It would require only that either the descending or the segmental inputs be organized with a different 'α–γ balance' for flexibility to exist during unrestrained motor behaviour.

In isometric voluntary contractions performed in a stereotyped manner, each spindle ending is activated at a contraction strength which is reproducible for the ending but which can differ markedly from those for other endings (Burke, Hagbarth & Skuse, 1978). This 'threshold for activation' results from the fusimotor influences acting on that particular ending, and probably reflects a recruitment threshold for the fusimotor neurones innervating the ending (Burke et al. 1978). Measurement of the threshold for spindle activation can therefore provide an indirect measure of the level of fusimotor drive directed to the contracting muscle relative to the degree of skeletomotor activity. The threshold is an expression of the 'α–γ balance'. The present study was undertaken to see whether manoeuvres which produce different descending influences or different segmental sensory inputs can alter the thresholds for activation of single spindle endings during an isometric voluntary contraction.

METHODS

The experimental data were collected in twelve successful experiments on seven healthy adult volunteers, all of whom had given informed consent to the experimental procedure. Three of the twelve experiments were performed on two of the authors. Of the other five subjects, three had volunteered previously for other studies, but all five were unaware of the purposes of the present study.

Neural recordings. Using standard techniques, unitary afferent potentials from forty-two spindle endings were recorded at the level of the fibular head from fascicles of the peroneal nerve innervating tibialis anterior, extensor digitorum longus, extensor hallucis longus and extensor digitorum brevis (cf. Vallbo et al. 1979). All afferent potentials were identified as of muscle spindle origin using electrically induced twitch contractions of the appropriate muscle.

Experimental procedures. Subjects lay supine with the foot secured in an isometric myograph which recorded the forces produced by the muscles operating at the ankle joint. The angle at the ankle joint was fixed initially in 16–22° plantar flexion. The ankle position could be adjusted between 0 and 25° plantar flexion in fixed steps of approximately 3°. With tibialis anterior afferents, the foot was secured between two transverse bars centered at the metatarsal heads to prevent movement of the ankle joint. With this position access to the toes was unimpeded so that

the toe extensor muscles could be subjected to further stretch or shortening. With toe extensor afferents, the transverse bars were extended so that they also prevented movement of the toes. A four-arm strain gauge bridge, bonded to the base-plate of the myograph, provided a measure of contraction torque. The electromyogram (e.m.g.) of the receptor-bearing muscle was recorded by a pair of needle electrodes insulated to within 2 mm of the tip, inserted into the muscle close to and on either side of the spindle ending, which was first located by punctate pressure applied to the muscle belly. The e.m.g. of triceps surae was recorded by surface electrodes 5 cm apart. All experimental data were monitored during the experiment and recorded on tape for subsequent analysis.

Before the neural recordings, the subjects were trained carefully to contract at will predominantly tibialis anterior or the toe extensor muscles, given visual feed-back of contraction torque and, occasionally, the e.m.g. of the appropriate muscle. Recordings were not made until the subject could generate a reproducible slowly increasing contraction of the chosen muscle, with or without feed-back of contraction torque. During recordings, the threshold for activation for each spindle ending was determined in a slowly developing isometric contraction, and the reproducibility of this threshold checked. The subjects then repeated the same contraction during various conditioning manoeuvres which were designed (i) to activate descending pathways from higher centres (the Jendrassik reinforcement manoeuvre; vestibular stimulation; head rotation, with or without movement of the arms), or (ii) to provide a segmental sensory input (non-nociceptive cutaneous stimulation; stretch or shortening of synergists; activation of muscle afferents from antagonistic muscles; ankle position changes). In some instances (cf. Fig. 3), the 'conditioning' manoeuvre was applied during the test contraction. Extreme care was taken to ensure that each subject performed the test contractions during the conditioning manoeuvres as in the control sequences. Results were discarded during the recording when the pattern of muscle activation differed overtly from the control. An altered pattern of muscle activation could sometimes be detected by a change in e.m.g. activity for a given torque level, suggesting that other muscles operating at the ankle joint were contracted unintentionally.

Conditioning manoeuvres. Each conditioning manoeuvre was tested in isolation in the passive relaxed state to determine whether it was capable of activating skeletomotor or fusimotor neurones directly. Subjects performed the *Jendrassik reinforcement manoeuvre* by interlocking their hands and attempting to pull them apart against their own resistance using near-maximum effort. Performance of this manoeuvre is well known clinically to potentiate proprioceptive reflexes of muscles remote from those actually contracting in the manoeuvre. *Vestibular stimulation* was achieved by irrigation of the external auditory meatus with water maintained at 44–47 °C or 30 °C using a flow rate of 300 ml/min. The electro-oculogram was recorded during these tests using a pair of surface electrodes secured to the nasion and to the outer canthus of one eye. The head was supported, flexed 30° from the horizontal so that the lateral semi-circular canal was in the vertical plane. The eyes were kept closed. *Head rotation* was performed either passively by the experimenters or actively by the subject, the trunk, neck and head lying in the same longitudinal plane, usually horizontal. To produce non-nociceptive *cutaneous stimulation*, vibration at 70 Hz was applied to the skin through a large piece of foam rubber using a pneumatic vibrator driven by compressed air. The amplitude of the unloaded vibrator's oscillation exceeded 2 mm. The foam rubber was designed to increase the cutaneous area stimulated by the vibration. When recording from tibialis anterior afferents, *lengthening or shortening of synergists* was produced by passive movements of the toes (see earlier). With toe extensor afferents, the only form of stretch that could be applied to tibialis anterior selectively was direct pressure on the tendon of tibialis anterior. With one afferent in extensor digitorum brevis, stretch of synergists was produced by ankle position changes. *Activation of triceps surae muscle afferents* was achieved by the application of vibration to or by direct pressure on the Achilles tendon.

RESULTS

Of the forty-two spindle endings, thirty-seven could be activated in the control voluntary contractions. Control contractions were usually only to the force required to activate the ending; the strongest contraction in this study was 12 Nm, representing 25–30 % maximum voluntary power for that subject. For the thirty-seven

endings, the thresholds for spindle activation in these contractions ranged from less than 0·5 to 7·0 Nm.

The conditioning manoeuvres which most consistently altered the thresholds for spindle activation were vestibular stimulation, cutaneous stimulation and proprioceptive stimuli. These conditioning manoeuvres commonly changed the thresholds by a factor of two relative to the control threshold. However, the changes were small in absolute terms and when expressed as a percentage of maximum voluntary power. In general, for those endings which already had very low thresholds, further lowering could not be demonstrated: with none of the conditioning manoeuvres were endings activated in advance of the initial e.m.g. potentials of the test contractions. With the exception of vibration (which directly activated some spindle endings), none of the conditioning manoeuvres was sufficient by itself to produce spindle acceleration.

Supraspinal influences

Jendrassik reinforcement manoeuvre. With seven of nine spindle endings performance of strong reinforcement manoeuvres did not alter the background discharge. With the remaining two endings, transient acceleration occurred in association with a
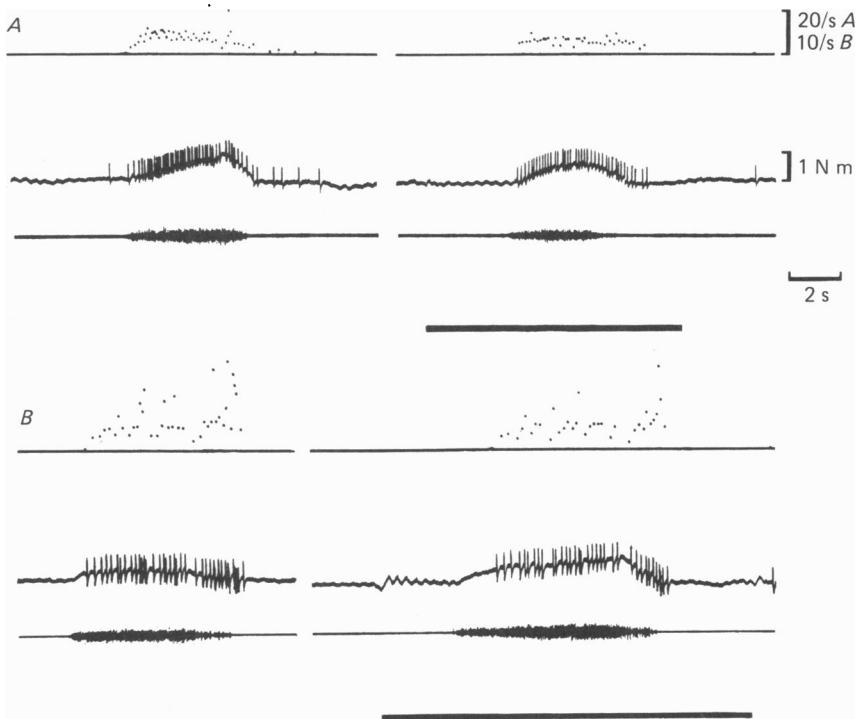

Fig. 1. The effects of the Jendrassik reinforcement manoeuvre on thresholds for voluntary activation of two primary endings (*A* and *B*), both in long toe extensors. The traces on the left were obtained during control isometric voluntary contractions. On the right, test contractions performed during the Jendrassik manoeuvre (indicated by horizontal bars). The manoeuvres were vigorous, produced transient torque disturbances, especially in *B*, but did not directly activate the endings. During the manoeuvre, the threshold for activation of spindle *A* is unaltered; that of spindle *B* is slightly elevated. Traces in *A* and *B* are: instantaneous frequency of spindle discharge; torque at the ankle joint, to which a standard pulse representing each spindle afferent potential has been added; e.m.g. of the receptor-bearing muscle.

change in torque at the ankle joint. No detectable e.m.g. activity accompanied the change in torque, which might therefore have been caused by passive displacement of the body. A torque change resulting from active contraction cannot be completely excluded because potentials from motor units remote from the e.m.g. needle electrodes could have escaped detection. With seven of eight endings for which it was
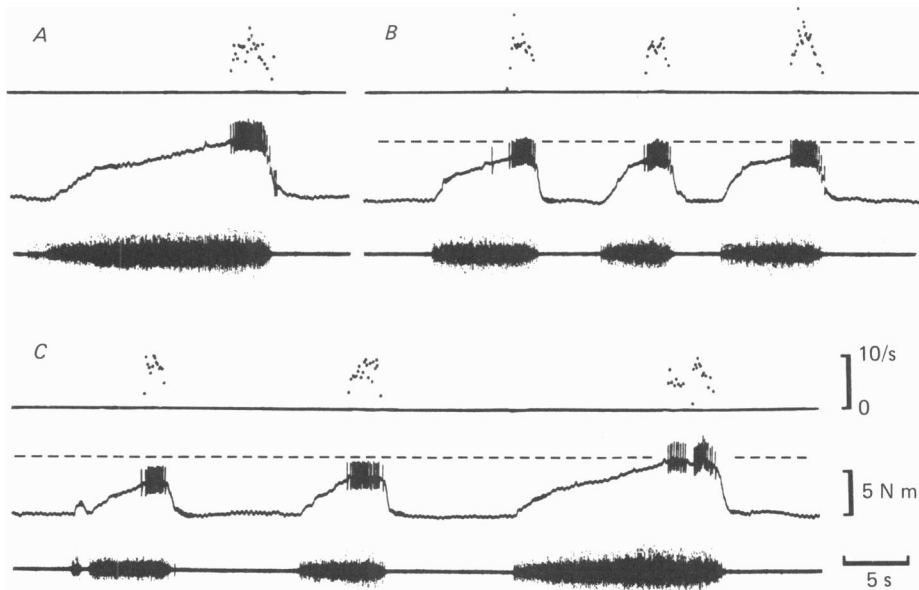

Fig. 2. The effects of caloric vestibular stimulation on the threshold for voluntary activation of a primary ending in tibialis anterior. *A*, control isometric voluntary contraction, with spindle activation occurring at 5–6 Nm. *B*, test contractions performed during irrigation of the ipsilateral ear with warm water. The first contraction was performed 40 sec after the onset of the irrigation when the subject was experiencing vertigo. *C*, contractions performed after cessation of irrigation, showing gradual recovery of the threshold for spindle activation to that seen in *A*. The first of these contractions was performed 40 sec after cessation of irrigation and is associated with a lower threshold than during irrigation. In *B* and *C*, the interrupted line indicates the force level at which the spindle was activated in the control contractions (cf. *A*). Traces are as in Fig. 1.

tested, the threshold for spindle activation was not altered when the test contractions were performed during the Jendrassik manoeuvre (Fig. 1*A*). (In Figs. 1 and 2, a standard pulse representing each spindle potential was electronically added to the torque record to illustrate threshold changes more clearly.) With the eighth ending the threshold was elevated slightly on the two occasions it was tested (Fig. 1*B*). Thus, reinforcement manoeuvres do not appear to alter the 'α–γ balance' in favour of fusimotor neurones. It is therefore concluded that these manoeuvres do not activate fusimotor neurones selectively or have a demonstrable bias in favour of fusimotor neurones.

Vestibular stimulation was performed during recordings from eleven spindle endings. Irrigation of the ipsilateral ear with warm water sufficient to produce vertigo altered the thresholds for voluntary activation of eight endings, although by itself the irrigation had no detectable effect on skeletomotor activity or resting spindle discharge. With six of the eight endings the stimulation lowered the thresholds for

activation during the irrigation. This effect on the threshold increased during the irrigation, and generally outlasted it by 75–90 sec, with gradual reversal to the previously established control threshold (Fig. 2). For two endings the greatest lowering of the threshold was seen in contractions performed after the cessation of irrigation. With the remaining two endings there were no significant changes during irrigation but following its cessation the thresholds for activation were transiently elevated.

Similar changes in spindle thresholds resulted from irrigation of the contralateral ear, but these effects were less prominent. With two spindle endings irrigation with cold water produced qualitatively similar effects as irrigation with warm water.

Head rotation had no detectable effects by itself on skeletomotor or fusimotor activity during recordings from five endings, whether the rotation was performed passively or actively. With one ending in tibialis anterior a small but reproducible lowering of the threshold for voluntary activation occurred during passive rotation of the head and neck to either side. Voluntary changes in limb position (extension of the limb on the side to which the head was rotated, with flexion of the opposite limb) displaced the body, thus altering the torque at the ankle joint and presumably the degree of stretch on spindle endings. When this manoeuvre was performed without such changes the thresholds for spindle activation were not detectably altered.

Segmental influences

Cutaneous stimulation. Vibration applied to the dorsum of the ispilateral foot clear of the tendons of the receptor-bearing muscles increased the background discharge of three of seventeen spindle endings. However, the three endings discharged at subharmonics of the vibration frequency (70 Hz), indicating that the increase in discharge represented direct activation due to spread of the vibratory stimulus to the spindles rather than indirect activation via the fusimotor system. With seven of the seventeen endings the thresholds for voluntary activation in test contractions were lowered during similar vibration (Fig. 3). These effects were presumably mediated indirectly since the increased discharge was not harmonically related to the vibration frequency, as would have occurred had the voluntary contraction merely potentiated the vibration sensitivity of the endings (cf. Burke, Hagbarth, Löfstedt & Wallin, 1976). Five of the seven endings that had a lower threshold during vibration of the dorsum of the foot were in tibialis anterior. Seven of the ten endings whose thresholds were unaffected were in the long toe extensors.

With four endings, vibration was applied to the plantar surface of the ipsilateral foot, usually laterally, immediately distal to the heel. Vibration by itself did not excite the endings. The thresholds for activation in test contractions were raised with three endings (two in extensor hallucis longus; one in extensor digitorum longus), and unaltered with the fourth (extensor digitorum longus).

Struppler & Velho (1976) reported that scratching the dorsal and plantar surfaces of the foot with a needle is sufficient to activate secondary but not primary spindle endings in tibialis anterior of normal subjects. The apparent discrepancy with the present findings could be due to differences in the cutaneous receptor populations activated in the studies: mechanoreceptors in the present study; presumably nociceptors in the report of Struppler & Velho. Why only secondary endings were activated by the presumably nociceptive stimulus is not clear.

Proprioceptive stimuli. With nine spindle endings (seven in the toe extensor muscles; two in tibialis anterior), passive stretch of the receptor-bearing muscle was produced by plantar flexion of the ankle joint. With five endings, this manoeuvre had no detectable effect; with four endings the threshold forces required for voluntary activation were elevated in the more plantar-flexed position (Fig. 3A and B). The effects of passive stretch of synergistic muscles were tested with nine spindle endings (seven in tibialis anterior; one each in extensor digitorum brevis and longus). The thresholds for voluntary activation of three endings were elevated by the manoeuvre, and that of a fourth ending was lowered. No significant effect was seen on the thresholds of the remaining five endings.

Vibration was applied to the Achilles tendon during recordings from fourteen spindle endings. Five were activated at subharmonics of the vibration frequency due to spread of the vibratory
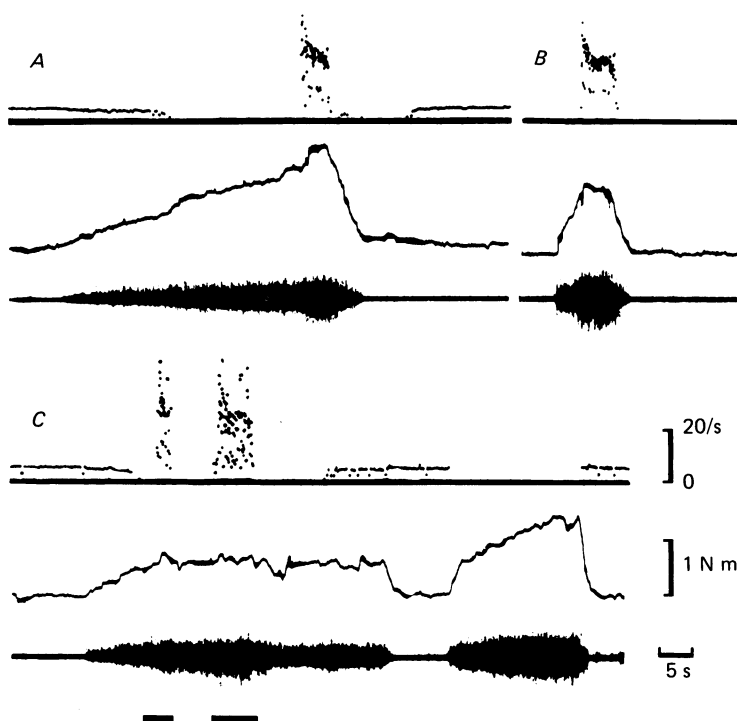

Fig. 3. The effects of ankle joint rotation and cutaneous vibration on the threshold for voluntary activation of a spindle ending in tibialis anterior. *A*, isometric voluntary contraction with tibialis anterior stretched (ankle joint in 22° plantar flexion). *B*, isometric voluntary contraction with tibialis anterior shorter (ankle joint in 16° plantar flexion). Note the absence of background spindle discharge and the displacement of the torque base-line. The threshold for spindle activation is lower than in *A*. *C*, cutaneous vibration at 70 Hz (indicated by horizontal bars) applied during an isometric voluntary contraction with ankle joint in 22° plantar flexion. The ending is activated during vibra-tion, the torque level being much lower than the threshold for activation in *A*. Note that spindle discharge is not at a subharmonic of 70 Hz. In a subsequent stronger contraction without vibration the ending is not activated; the contraction level does not reach the threshold shown in *A*. Traces are as in Fig. 1, except that the spindle pulse has not been added to the torque trace. The occasional frequency dots at half the true frequency are present because on these occasions the afferent potential did not exceed the trigger level for the frequency meter.

stimulus. With a further two endings the neural recordings became contaminated by e.m.g. potentials from triceps surae due to the development of a strong tonic vibration reflex. During vibration of the Achilles tendon, the thresholds for voluntary activation of two spindle endings were lowered, a similar but more equivocal effect was seen with a third ending, and there was no definite change with the remaining endings. Maintained firm pressure on the Achilles tendon lowered the thresholds for voluntary activation of two of the four spindle endings on which the manoeuvre was tested.

Other manoeuvres

Co-contraction of antagonistic muscles acting on the ankle joint was tested during recordings from seven endings, but the results were difficult to interpret because the subjects were required to tense the limb, thus negating the value of the torque recording as an indication of contraction strength. However, compared with control contractions, one ending could not be activated in co-contractions until significantly more e.m.g. had developed in the receptor-bearing muscle. With a second ending, a stronger contraction (as judged by the intensity of the e.m.g. activity recorded from the receptor-bearing muscle) produced a spindle discharge of lower frequency than in the control contractions.

DISCUSSION

The present findings suggest that it is possible to vary the relative proportions of fusimotor and skeletomotor activity directed to a muscle when it is contracting voluntarily. Thus, the human nervous system is not committed to a rigid form of fusimotor control little better than the skeleto-fusimotor (β) system of amphibia. However, there appear to be limitations to this flexibility: evidence for complete dissociation of the skeletomotor and fusimotor drives to the contracting muscle has not been seen, except perhaps as a threshold phenomenon (cf. Burke, McKeon, Skuse & Westerman, in preparation), or during stretch reflex contractions (Burke *et al.* 1976).

It is important to realize that the threshold for activation of a spindle ending in a voluntary contraction is only a relative measure of the fusimotor influences acting on that spindle. For example, a decrease in the threshold could result from greater excitation of fusimotor than skeletomotor neurones or from greater inhibition of skeletomotor than fusimotor neurones. The failure to demonstrate a change in the threshold (much as occurred with the Jendrassik reinforcement manoeuvre) will occur if the effects exerted are so similar to those of a voluntary contraction that they do not alter the 'α–γ balance' present in the contraction. Additionally, it cannot be claimed that the effects on afferent discharge which are documented in the present study are necessarily those which would occur under all other conditions: voluntary contraction of a muscle could be associated with changes in the functional state of spinal cord circuitry, and this might conceal reflex effects operative under other circumstances. However, if the skeletomotor effects of a stimulus are known, it should be possible to draw valid conclusions about the fusimotor effects of that stimulus from a change in the threshold for spindle activation. Furthermore, as was the case in the present study, weak stimuli which are insufficiently intense to discharge the motoneurone pools in the relaxed state may have demonstrable effects when the motoneurone pools have been raised to firing threshold.

Underlying mechanisms. Since non-specific arousal accompanying the Jendrassik reinforcement manoeuvre did not alter the 'α–γ balance' in favour of fusimotor neurones, it is likely that the lowering of spindle thresholds produced by caloric vestibular stimulation was the result of vestibular stimulation rather than a non-

specific alerting effect of the irrigation. Persistence of the effects for up to 1·5 min supports this view. In the cat, direct stimulation of the vestibular nerve or of the branch innervating the lateral semi-circular canal activates α and γ motoneurones of tibialis anterior and gastrocnemius bilaterally; low intensity stimulation activates γ motoneurones selectively (Gernandt, 1967; cf. also Diete-Spiff, Carli & Pompeiano, 1967; Grillner, 1969). In relaxed human subjects, caloric vestibular stimulation enhances proprioceptive reflexes of lower limb extensor muscles, the degree of enhancement of quadriceps reflexes being greater on the ipsilateral side (Eklund & Hagbarth, 1966; Delwaide, 1977). Such stimulation also produces weak potentiation of biceps femoris reflexes, but has no significant effect on tibialis anterior reflexes (Delwaide, 1977). In the present experiments, a voluntary contraction was used to raise the motoneurone pools above firing threshold and so to unmask effects not demonstrable in the relaxed state. The caloric stimulation probably represented low intensity vestibular stimulation, which, by analogy with the results of Gernandt (1967), would excite predominantly fusimotor neurones – hence the lowering of the thresholds for spindle activation.

The changes induced by cutaneous vibration cannot with certainty be attributed solely to cutaneous receptors because mechanoreceptors in the small muscles and the joints of the foot could have also been activated. Nevertheless, the spindle response patterns evoked by such stimulation are comparable with the effects of tactile and nociceptive cutaneous stimuli at equivalent sites in spinal and decerebrate cats (Hunt, 1951; Eldred & Hagbarth, 1954; Hunt & Paintal, 1958; cf. also Grillner, 1969). In these preparations direct effects on skeletomotor and fusimotor neurones occurred but those on fusimotor neurones were of lower threshold. In normal human subjects, cutaneous reflexes elicited by stimulation of cutaneous nerve or of the skin area itself have an essentially similar pattern to that seen in the present study (Hagbarth, 1960; Kugelberg, Eklund & Grimby, 1960; Bathien & Bourdarias, 1972; Hugon, 1973). Thus, 'cutaneous' mechanoreceptor afferents probably affect both the α and γ motoneurone pools, but the present results suggest that their effects are biased more in favour of γ motoneurones, a conclusion in keeping with the earlier findings in the cat. The feed-back from cutaneous mechanoreceptors appears to play a very important role in motor control (cf. for example, Marsden, Merton & Morton, 1977; Gandevia & McCloskey, 1977; Abbruzzese, Hagbarth, Homma & Wallin, 1978; Hulliger, Nordh, Thelin & Vallbo, 1979). The present findings would support this view.

Functional implications. The results of vestibular stimulation indicate that different systems can activate α and γ motoneurones in different proportions. In the upper limb, limb girdle muscles are normally involved in postural fixation and are controlled by descending systems distinct from those primarily activated in discrete manipulation (cf. for example, Kuypers, 1973). It is therefore probable that the α–γ linkage will differ for different muscles during any one motor act, depending on the extent to which those muscles are used as prime movers or as a postural fixators (cf. Loeb & Duysens, 1979). For any one muscle, a change in role from prime mover to postural fixator during the course of a movement would probably necessitate a change in the 'α–γ balance'. Changes in the peripheral feed-back from cutaneous and muscle mechanoreceptors such as would occur during manipulative behaviour would also

alter the balance of the skeletomotor and fusimotor drives directed to the contracting muscle. The 'α-γ linkage' may well appear rigid when a voluntary motor act is performed repeatedly in a stereotyped manner, but a systematic flexibility in the linkage will be introduced as more degrees of freedom are allowed, with greatest expression in the freely moving animal (cf. Prochazka, Westerman & Ziccone, 1977; Loeb & Duysens, 1979). Thus, it seems that the efferent innervation of a contracting muscle will be modified *appropriately* during the progress of a motor act both by changes in the central programme and by changes in the sensory feed-back coming from the exploring limb.

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