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Kinaesthetic Role of Muscle Afferents in Man, Studied by Tendon Vibration and Microneurography

J. P. Roll[1] and J. P. Vedel[2]

[1] Laboratoire de Psychophysiologie, Université Aix-Marseille, Centre de Saint-Jérôme, F-13397 Marseille Cedex 4, France
[2] C.N.R.S.-INP 4, B.P. 71, F-13277 Marseille Cedex 9, France

Summary. The characteristics of vibration-induced illusory joint movements were studied in healthy human subjects. Unseen by the subject, constant frequency vibration trains applied to the distal tendon of the Triceps or Biceps induced an almost constant velocity illusory movement of the elbow whose direction corresponded to that of a joint rotation stretching the vibrated muscle. Vibration trains of the same duration and frequency applied alternatively to the Biceps and Triceps evoked alternating flexion-extension illusory movements.

During successive application of vibration trains at frequencies from 10 to 120 Hz, the perceived velocity of the illusory movements increased progressively from 10 to 70–80 Hz, then decreased from 80 to 120 Hz. The maximal perceived velocity was three times higher during alternating vibration of the Biceps and Triceps than during single muscle stimulation.

Unit activity from 15 muscle spindle primary endings and five secondary endings located in Tibialis anterior and Extensor digitorum longus muscles were recorded using microneurography in order to study their responses to tendon vibration and passive and active movements of the ankle.

Primary endings were all activated by low amplitude tendon vibration (0.2–0.5 mm) previously used to induce illusory movements of the elbow. The discharge of some was phase-locked with the vibration cycle up to 120 Hz, while others responded one-to-one to the vibration cycle up to 30–50 Hz, then fired in a sub-harmonic manner at higher frequencies. Secondary endings were much less sensitive to low amplitude tendon vibration.

Primary and secondary ending responses to ramp and sinusoïdal movements of the ankle joint were compared. During the movement, the primary ending discharge frequency was almost constant, while the secondary ending activity progressively increased. During ankle movements the primary ending discharge appeared mainly related to velocity, while some secondary activities seemed related to both movement velocity and joint angle position.

Muscle spindle sensory ending responses to active and passive ankle movements stretching the receptor-bearing muscle (plantar flexion) were qualitatively and quantitatively similar. During passive reverse movements (dorsiflexion) most of the sensory endings stopped firing when their muscle shortened. Active muscle shortening (isotonic contraction) modulated differently the muscle spindle sensory ending discharge, which could stop completely, decrease or some times increase during active ankle dorsiflexion. During isometric contraction most of the muscle spindle sensory endings were activated.

The characteristics of the vibration-induced illusory movements and the muscle spindle responses to tendon vibration and to active and passive joint movements strengthened the possibility of the contribution of primary endings to kinaesthesia, as suggested by several previous works. Moreover, the present results led us to attribute to proprioception in the muscle stretched during joint movement a predominant, but not exclusive, role in this kind of perception.

Key words: Kinaesthesia – Muscle afferents – Tendon vibration – Microneurography – Man

Introduction

The contribution of muscle spindles to conscious perception of joint movement and position in Man has been extensively discussed in recent years (Mountcastle et al. 1952; Brindley and Merton 1960; Gelfan and Carter 1967; Goodwin et al. 1972;

Offprint requests to: Dr. J. P. Roll (address see above)

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Matthews 1977). Two of the most important works in this field were those of Eklund (1972) and of Goodwin et al. (1972) which, independently, showed that mechanical vibration applied to muscle tendons in man induced errors in the appreciation of joint position and, moreover, produced illusions of movement. The main conclusion of the work of Goodwin et al. was "that muscle receptors do contribute to position sense". This conclusion represents, in a historical perspective, a complete reversal with regard to the classical view which considered that the conscious perception of movement was related to joint afferents (Mountcastle and Powell 1959) and/or to the so called "corollary discharge" (Sperry 1950). The experimental results which have led to the exclusion of the eventual contribution of muscle proprioception to kinaesthesia and position sense have been extensively analysed in recent reviews (McIntyre 1977; Matthews 1977; McCloskey 1978; Roland 1978) and are mainly related to three findings:

Firstly, cortical projections from group I muscle afferents were not found in the cat (Lloyd and McIntyre 1950; McIntyre 1953; Mountcastle et al. 1952) whereas those from joint afferents were adequately demonstrated (Rose and Mountcastle 1959).

Secondly, anaesthesia of finger joint afferents in man, preserving muscle innervation, resulted in a loss of both kinaesthesia and position sense (Browne et al. 1954; Provins 1958; Chambers and Gilliat 1954).

Thirdly, the demonstration that extraocular muscle stretch as well as somatic muscle stretch in awake man did not induce any sensation of movement or of position. From these data and their own observations, Brindley and Merton (1960) and Gelfan and Carter (1967) concluded in the same way that "the eye has no position sense", and concerning the somatic muscles, that "there is no muscle sense".

At the same time, if the role of muscle receptors in the medullary and sub-cortical loops involved in motor regulation was extensively discussed, the ability of muscle spindles to give correct information about the absolute length and length changes in muscle was not so well accepted. It was considered that conscious perception was mainly relevant on joint afferents (Boyd and Roberts 1953; Mountcastle et al. 1952). However, further experiments showed that the movement coding by joint afferents appeared to be limited to extreme positions of the joint (Burgess and Clark 1969; Grigg 1975), but these results were recently disputed by the work of Ferrel (1980).

At present, the contribution of muscle spindles to kinaesthesia suggested by the observation of Goodwin et al. (1972) is supported by the well established cortical projections of muscle afferents in both cats and primates (Oscarsson and Rosen 1963; Albe-Fessard and Liebeskind 1966; Landgren and Silfvenius 1966; Phillips et al. 1971) and by the demonstration by Burke et al. (1976) that tendon vibration in man is a powerful stimulus for muscle spindles, suggesting that these proprioceptors could be responsible for the illusion of movement evoked by such mechanical stimulation. Recent observations have also demonstrated that pulling upon exposed muscle tendon in awake man induced sensations of joint movement (Matthews and Simmonds 1974) and that kinaesthesia persisted after elimination of joint signals by local anaesthesia (Goodwin et al. 1972).

The present work is an attempt to support the hypothesis of a primary role in kinaesthesia played by the proprioception of the muscle stretched during joint movement. In the first part the quantitative relationships between the frequency of tendon vibration and the parameters of the illusory movements have been extensively studied in different experimental situations. In the second part, the microneurography method (Hagbarth and Vallbö 1968), which makes possible the recording of single unit afferent activities from muscle mechanoreceptors in man, has been used:

1. To define, in our experimental conditions, which receptors were preferentially activated by tendon vibration, in order to determine the nature of the afferent patterns underlying the illusory sensations of movements.
2. To systematically study the characteristics of the spindle afferent discharge when the receptor bearing muscle is lengthened or shortened by passive or active movements, in order to determine to what extent the proprioceptive patterns are representative of the joint movement parameters and to determine the eventual relationships between the vibratory patterns inducing illusion of movement and the characteristics of the spindle responses to real joint movements.

The present results show that the tendon vibration frequency modulates the illusory movement quantitatively and, moreover, suggest the essential but probably not exclusive role in kinaesthesia of the muscle spindle afferent patterns originating from the stretched muscle during joint movement.

Material and Methods

Effects of Tendon Vibration

Material. The study of the illusion of movement induced by tendon vibration was carried out on 12 healthy adults ranging in age from

24 to 40. Six served as subjects in experiments on single vibration (vibrations applied to one muscle) and the six others in experiments on double vibrations (vibrations applied to the two antagonistic muscles of the elbow). Figure 1 illustrates the experimental setup: the subject was seated in a comfortable armchair, with his hands and forearms lying in an horizontal position on symmetrical devices. The forearm supports were articulated at the elbow by a low inertia mechanical system which could be immobilized in any given position. Prior to the experiments, each subject was trained to track with one forearm, and without vision, various passive movements imposed on the other forearm. In this situation, passive movements were imposed using a DC motor connected to the forearm support. During the vibration sequences, the subject was asked to track with the right forearm the illusory movements perceived by the left forearm whose support was completely rigid.

The angular positions and movements of the tracking forearm were recorded by a linear potentiometer. Eventual EMG activity of the Biceps and Triceps brachii were recorded by means of silver surface electrodes. The EMG and potentiometer signals were amplified and recorded on an ink-writer.

Tendon Stimulation. Mechanical vibrations were applied perpendicularly to the distal tendons of the Triceps and/or Biceps brachii. They were delivered by one or two electromagnetic devices (Ling Dynamic Systems, Type 201) fixed on independent holders. The vibrating devices were driven by rectangular pulses (2.5 ms) delivered by a neuro-stimulator (GRASS 588), coupled to a power amplifier (L.D.S. Type 025). The amplitude of the vibrations was measured using an accelerometer included in the vibrator head. It varied from 0.2 to 0.5 mm from one experiment to another, but was maintained constant in the same experiment whatever the vibration frequency. The frequency used varied from 10 to 120 Hz; they were presented to the subject in a pseudo-random order. During an experimental session each frequency was presented three or four times. The mean velocity values of the tracking movements were automatically calculated for each frequency of vibration. Alternating vibratory stimulations of the Biceps and Triceps were delivered by two identical vibrators alternately triggered by pulse trains whose sequences were previously recorded on tape. In this situation, the duration of each vibration train was of 0.5, 1, or 2 s, and the mean velocity of the flexion phase was averaged over ten successive movements.

Microneurography

Material. Experiments were performed on 25 healthy subjects aged 18–43, all of whom had given informed consent to the experimental procedure. The subject was seated in a comfortable armchair. The legs were positioned in cushioned grooves permitting the maintenance of a stereotyped relaxed position without any muscular activity.

The right foot lay on a stationary plate, the left foot being fixed on a rotating pedal whose axis was centered in front of the ankle joint. The rotating pedal was:

either completely free in order to be able to move the ankle manually or to ask the subject to perform a voluntary movement,

or fixed in a given position and attached to a strain gauge bridge in order to measure the torque produced during isometric contraction of the muscle acting on the ankle joint,

or connected to an electromechanical device allowing ramp or sinusoïdal angular movements, variable in amplitude and velocity, to be imposed on the ankle joint.

Movements of the rotating pedal were recorded using a linear potentiometer. The position of the investigated leg was stereotyped from one experiment to another. The knee joint angle was about 120°–130°, the position of 90° at the ankle joint was taken as the zero position from which passive movements were imposed.

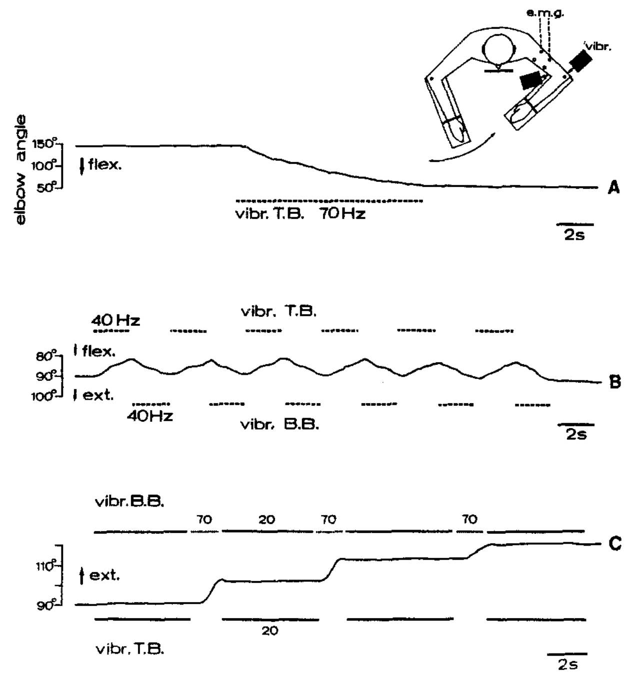

Fig. 1A–C. Illusory movements of the elbow joint induced by different patterns of mechanical vibration applied to the tendon of the Biceps brachii (BB) and Triceps brachii (TB) muscles. Vibration trains are applied to the left arm, the perceived movements are reproduced by the right arm (tracking arm) and recorded using a linear potentiometer. **A** Flexion movement perceived by the subject during vibration of the Triceps at 70 Hz. **B** Illusory flexion and extension movements evoked by alternate vibration (40 Hz) of the Triceps and Biceps muscles. **C** Simultaneous stimulation of the BB and TB at the same frequency (20 Hz) never induces any sensation of movement. The interruption of such a vibratory pattern by a vibration train (70 Hz) selectively applied to the BB induces an illusory extension movement. At the end of the BB stimulation, the new joint position perceived by the subject depends only on the amplitude of the preceding illusory movement and is not modified when the simultaneous vibration (20 Hz) of both muscles is again applied. Selective BB stimulation applied several times determines the perception of an increasingly extended position of the elbow

Recording Procedure. Muscle afferent activity from the Tibialis anterior (TA) and Extensor digitorum longus (EDL) was recorded from the lateral peroneal nerve at the level of the popliteal fossa. The nerve was localized by tactile exploration and percutaneous electrical stimulation inducing muscle contraction.

Single unit recording was performed using insulated tungsten microelectrodes (impedance 500 kΩ at 1 kHz, tip diameter around 5 μm) manually inserted percutaneously.

Microelectrode recording was continuously monitored on an oscilloscope and a loudspeaker making it possible to find nerve fascicle multi-unit activity responding preferentially to ankle joint plantar flexion. Single unit discharge was then isolated by manually adjusting the position of the electrode in minute steps. Neural activity was amplified successively by a Grass pre-amplifier (model P 15) and a Tektronix amplifier (model FM 122), then recorded on tape. The band width of the recordings was usually limited between 300 and 3,000 Hz to obtain optimal signal-to-noise ratio. Discharge frequency was calculated using an instantaneous rate meter. EMG activities from the Gastrocnemius-Soleus muscles

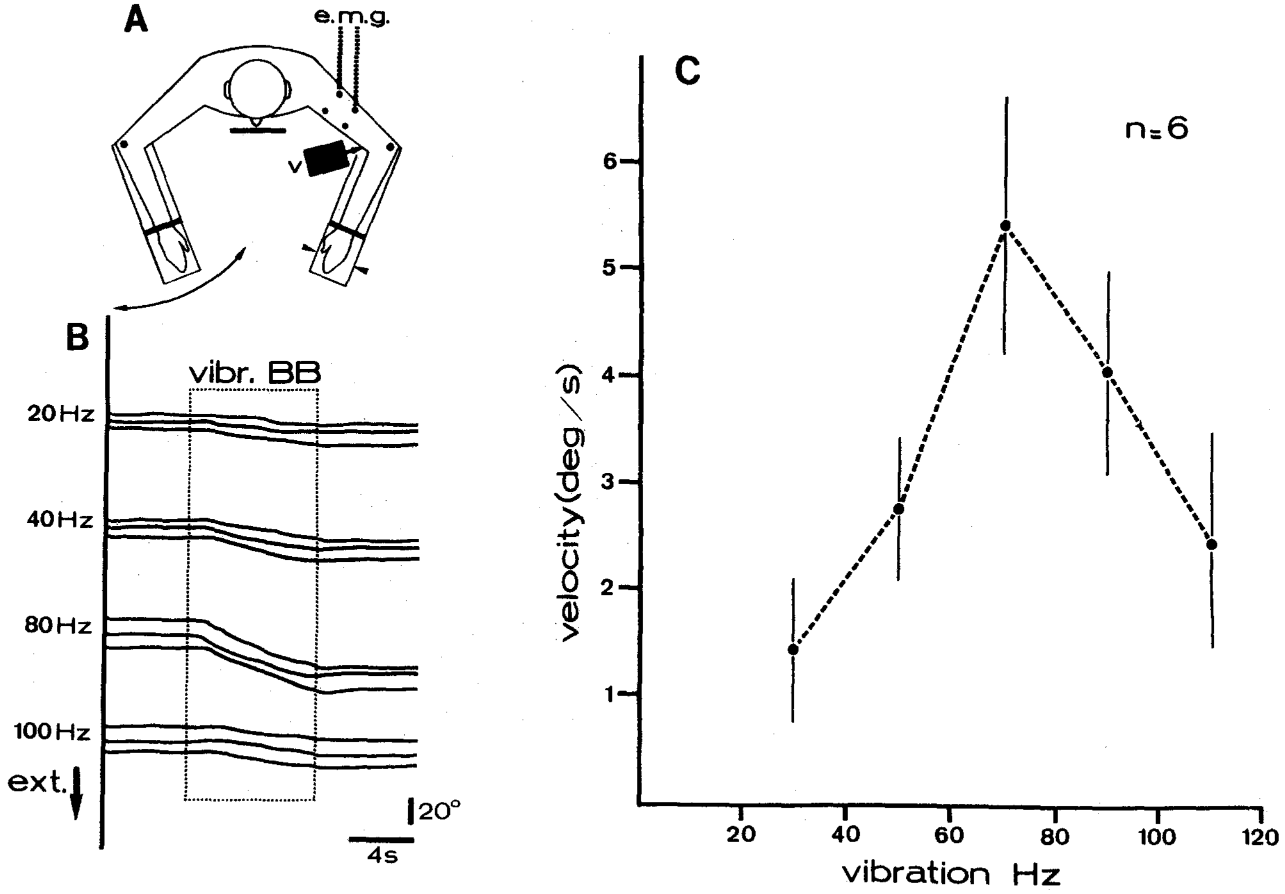

Fig. 2A–C. Illusory extension movement of the elbow perceived by the subject during tendon vibration of Biceps brachii (BB) at different frequencies. **A** Experimental conditions. Vibration is applied to the left arm whose elbow joint is immobilized. The perceived movements are reproduced by the right arm (tracking arm) and recorded using a linear potentiometer. **B** Characteristics of the illusory movements (reproduced by the tracking arm) perceived during BB vibration at 20, 40, 80, and 100 Hz. Vibration trains were applied three times at each frequency in the same experiment. **C** Relationship between vibration frequency and velocity of the illusory movement. The curve illustrates the mean results obtained from six subjects. Each point represents 18 trials. The confidence limits were calculated at 5%

and from the Tibialis anterior-Extensor digitorum longus muscles were recorded using surface electrodes.

Unit Identification. Twenty units have been classified as probable spindle sensory endings on the basis of their discharge characteristics; sensitivity to passive muscle stretch, tonic activity when the muscle was maintained at a constant length, decrease of activity during fast isotonic voluntary contraction, silent period during muscle twitch induced by transcutaneous electrical stimulation of the receptor muscle area.

Spindle sensory endings have been classified as possible primary or secondary on the basis of their responses to constant velocity joint movements, and their sensitivy to sinusoïdal movements of small amplitude. Moreover, the instantaneous frequency of the primary ending discharge appeared generally more variable than that of the secondary endings and, during a dorsiflexion shortening of the receptor-bearing muscle, the primary endings stopped firing just at the onset of the movement while the secondary ending activity decreased progressively. The response to vibration was not used as a criterion for the classification of afferent activity. Ten units were identified as slowly adaptating pressure receptors.

Results

Vibration-induced Illusion of Movement

Vibration Applied to a Single Muscle

When the elbow joint was immobilized, the application of a vibratory stimulus (60–80 Hz) to the distal tendon of the Biceps or Triceps brachii evoked an illusion of movement in all subjects. This illusion occurred whether the eyes were closed or open, but without the subject seeing the vibrated limb. Biceps stimulation resulted in an illusory movement of the forearm in extension, whereas Triceps stimulation resulted in an illusion of elbow flexion.

The sensations were similar to those felt when the vibrated muscle is stretched by a passively imposed elbow movement. Some subjects reported, at the end

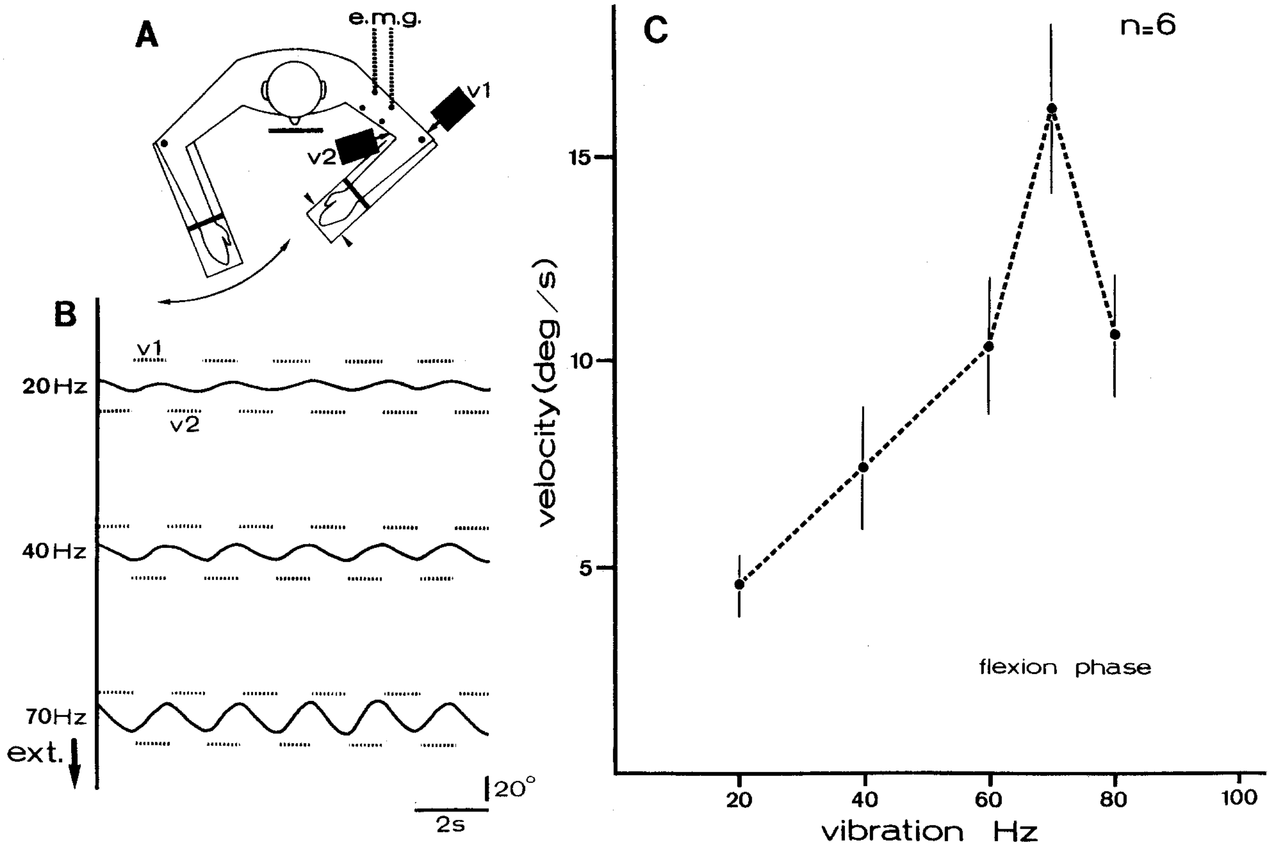

Fig. 3A–C. Illusory extension and flexion movements of the elbow induced by alternate vibration of Biceps brachii (BB) and Triceps brachii (TB) at different frequencies. **A** Experimental conditions. Vibration is applied to BB and TB in the left arm by means of two identical vibrating systems. The left elbow joint is maintained completely immobile. The perceived movements are reproduced by the right arm and recorded using a linear potentiometer. **B** Characteristics of the movements perceived by the subject during alternate vibration of BB and TB at 20, 40, and 70 Hz. **C** Relationship between vibration frequency and velocity of the flexion phase of the illusory movement. Each point of the curve has been calculated by averaging the results obtained from six subjects. Each point represents 24 trials. The confidence limits of the means were calculated at 1%

of the vibration train, the occurrence of an after-effect which consisted in a illusory reverse slow movement of the forearm towards its initial position.

An objective estimation of the parameters of the subjective movement was given by recording the movement of the contralateral tracking forearm (Fig. 1). All the results presented here have been obtained without any EMG activity in the vibrated muscle. According to the vibration frequency a light isometric contraction of the antagonistic muscle could occur.

Movement Velocity-Vibration Frequency Relationships. In all the subjects a vibration train at constant frequency applied for 10 s induced an almost constant velocity illusory movement. The mean velocity of the movement, for a given frequency, varied from one subject to another, but for a given subject the same vibration frequency applied several times in a random manner induced illusory movements of almost the same velocity. One example is illustrated in Fig. 2.

In all subjects, increasing the value of the vibration frequency from 10 to 70 Hz increased the perceived velocity of the illusory movement. An increase in vibration frequency from 80 to 120 Hz generally resulted in a decrease of the perceived velocity. Each individual curve is different in shape, but they all revealed that the perceived velocity reached a maximal value for a vibration frequency of about 60–80 Hz. Figure 2C illustrates the mean results obtained for six subjects. Each point represents 18 trials. The mean maximal velocity was obtained at 70 Hz and its mean value was about 5.5 degrees per second.

Alternating Vibration of Two Antagonistic Muscle

Vibration trains of the same frequency and duration alternately applied on the distal tendons of the

Biceps and Triceps muscles induced in all subjects an illusion of alternating extension and flexion of the forearm. Vibration of Biceps corresponded to the illusory extension phase while vibration of Triceps was related to the flexion phase.

Diagram A of Fig. 3 illustrates the experimental situation. In all subjects, the period of the alternating movements was strictly dependent on the duration of the vibration trains. The individual recordings presented in diagram B of Fig. 3 show that the amplitude of the movements reproduced by the tracking arm also increased when the frequency of the vibration trains increased from 20 to 70 Hz. This effect was obtained in all subjects. The duration of both the extension and flexion phases being identical for the different vibration frequencies applied, the progressive enhancement of the movement amplitude is the consequence of an increase in the perceived velocity related to the vibration frequency. Diagram C of Fig. 3 illustrates the results obtained from six subjects and shows the mean relationships existing between the frequency of vibration and the velocity of the flexion phases averaged over ten successive movements.

In the individual curves, as in the mean curve, an increase of the vibration frequency from 20 to 70 Hz resulted in an increase in the velocity of the movement, a decrease in the perceived velocity occurring above 80 Hz.

In all subjects, maximal velocity was obtained for a stimulation frequency of 70 Hz; however, the absolute value of this maximum was different from one subject to another and its mean value was about 16 degrees per second, i.e., approximately three times greater than the value obtained in the single vibration experiments.

Simultaneous Vibration of Two Antagonistic Muscles

In isometric conditions, the elbow angle being maintained at about 90–95°, the simultaneous application of identical vibratory stimuli (frequency and amplitude) to the distal tendons of the Biceps and Triceps did not induce any sensation of movement, but resulted in a sensation of stabilized position of the forearm similar to that perceived without vibration. This same sensation of stabilized position was perceived whatever the vibration frequency (between 20 and 100 Hz). So it appeared that the absolute frequency when the vibration trains were simultaneously applied to the two antagonistic muscles had no influence on the forearm position perceived by the subject.

During these experiments of simultaneous tendon vibration, if one of the stimulations was momentarily stopped and the other increased in frequency at the same time, the subject immediately perceived an illusory movement whose direction corresponded to that of a real movement stretching the vibrated muscle (Fig. 1C). Then, when the symmetrical vibrations were again applied, their common frequency being equal to or different from that previously used, the illusory movement stopped and the subject perceived a new illusory angle position of the forearm exclusively related to the end of the preceding illusory movement (Fig. 1C).

Microneurography Study of Muscle Spindle Activity in Man

For these experiments, anterior peritibial muscles (Tibialis anterior TA; Extensor digitorum longus EDL) were chosen, considering the sub-cutaneous course of their common nerve in the popliteal fossa and considering that vibration of their tendons induce illusions of movement of the ankle similar to those observed at the elbow level.

Sensory Activities Induced by Tendon Vibration

The effects of the tendon vibrations produced by the electromagnetic system used to obtain illusions of movement were observed on three kinds of mechanoreceptors.

Fifteen proprioceptive activities identified as those of muscle spindle primary endings appeared to be the most sensitive to vibratory stimuli. In the vibration frequency range used to evoke kinaesthetic effects (10–120 Hz), the primary endings were able to respond to each vibration cycle by one (Fig. 4C) or several spikes (two or three) without any adaptation. Occurrence of several spikes in response to one cycle increased when the vibration frequency was increased.

Figure 4A illustrates the response of a primary ending of TA driven by tendon vibrations from 10 to 100 Hz. Figure 4B shows that the same sensory ending can respond differently to two identical successive mechanical stimuli. From a given vibration frequency (60 Hz), the driven spindle activity abruptly decreases. Sensory ending discharge frequency then becomes a sub-harmonic of the vibration frequency (1/2 in this example). Since this effect is observed independently of any EMG activity in the vibrated muscle, it seems to depend on modification of the position of the vibrating system on the tendon. All primary endings recorded during vibration were able to respond one-to-one up to 30–50 Hz, but some

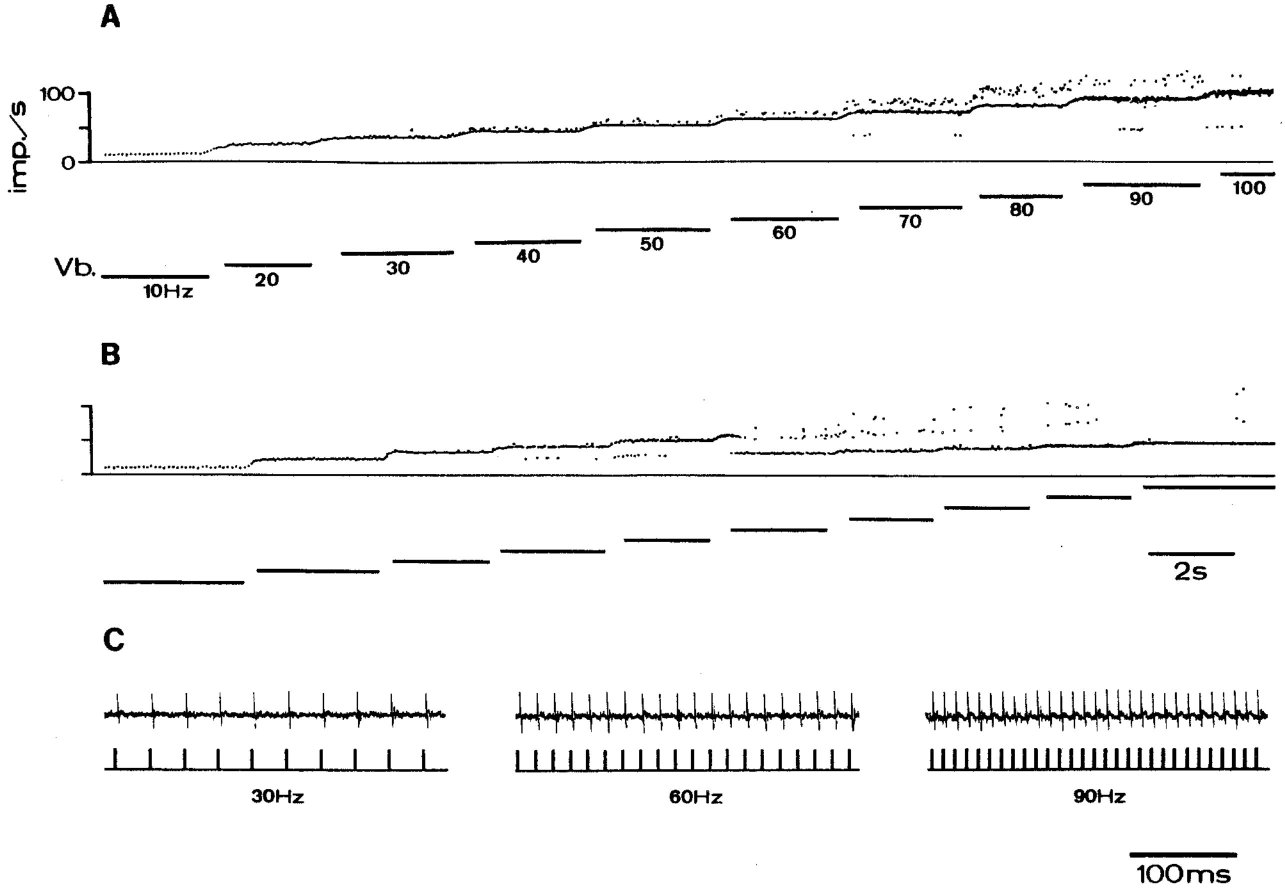

Fig. 4A–C. Driven activity (instantaneous frequency) of a spindle primary ending by mechanical vibration applied to the tendon of the receptor-bearing muscle (TA). **A** Optimal primary ending activation by tendon vibration from 10 to 100 Hz. **B** The same primary ending can eventually respond by a sub-harmonic discharge frequency to a particular vibration frequency (60 Hz in the example). **C** One-to-one primary ending responses to 30, 60, and 90 Hz tendon vibration

of them only fired in a sub-harmonic manner for higher frequencies whatever the position of the vibrating system on the muscle tendon.

Only vibrations precisely applied to the tendon of the receptor containing muscle were able to drive the primary endings. Vibration of the bone or skin near the tendon never increased the proprioceptive discharge. Maximal efficiency of the tendon vibration was obtained with ankle positions holding the muscle in stretch (from 90 to 95°).

Tendon vibration effects were also studied on five unitary activies identified as those of muscle spindle secondary endings. Their discharge was slightly increased by tendon stimulation but never followed the vibration cycles one-to-one and their instantaneous frequency never constituted a sub-harmonic of the vibration frequency. Two of the secondary endings recorded were completely insensitive to tendon stimulation by the vibrating system.

Ten mechanoreceptors identified as slowly adaptating pressure receptors and located in the anterior peritibial region were recorded. They all responded to pressure applied on a restricted area of skin covering TA and EDL muscles and their tendon, but their intramuscular localization was not confirmed. Vibration of the tendon of TA and EDL never drove this type of mechanoreceptor which was always silent in relaxed subjects. Nevertheless, these receptors were very sensitive to vibration directly applied to them. In this condition their discharge frequency was able to follow the vibration cycle one-to-one up to 200 Hz. The discharge of some of them was very slightly increased during muscle contraction and muscle stretch.

Characteristics of the Responses of Muscle Spindle Sensory Endings to Passive Joint Movement Imposed at Constant Velocity

When the ankle was maintained in a position of about 90°, approximately 60% of primary endings of

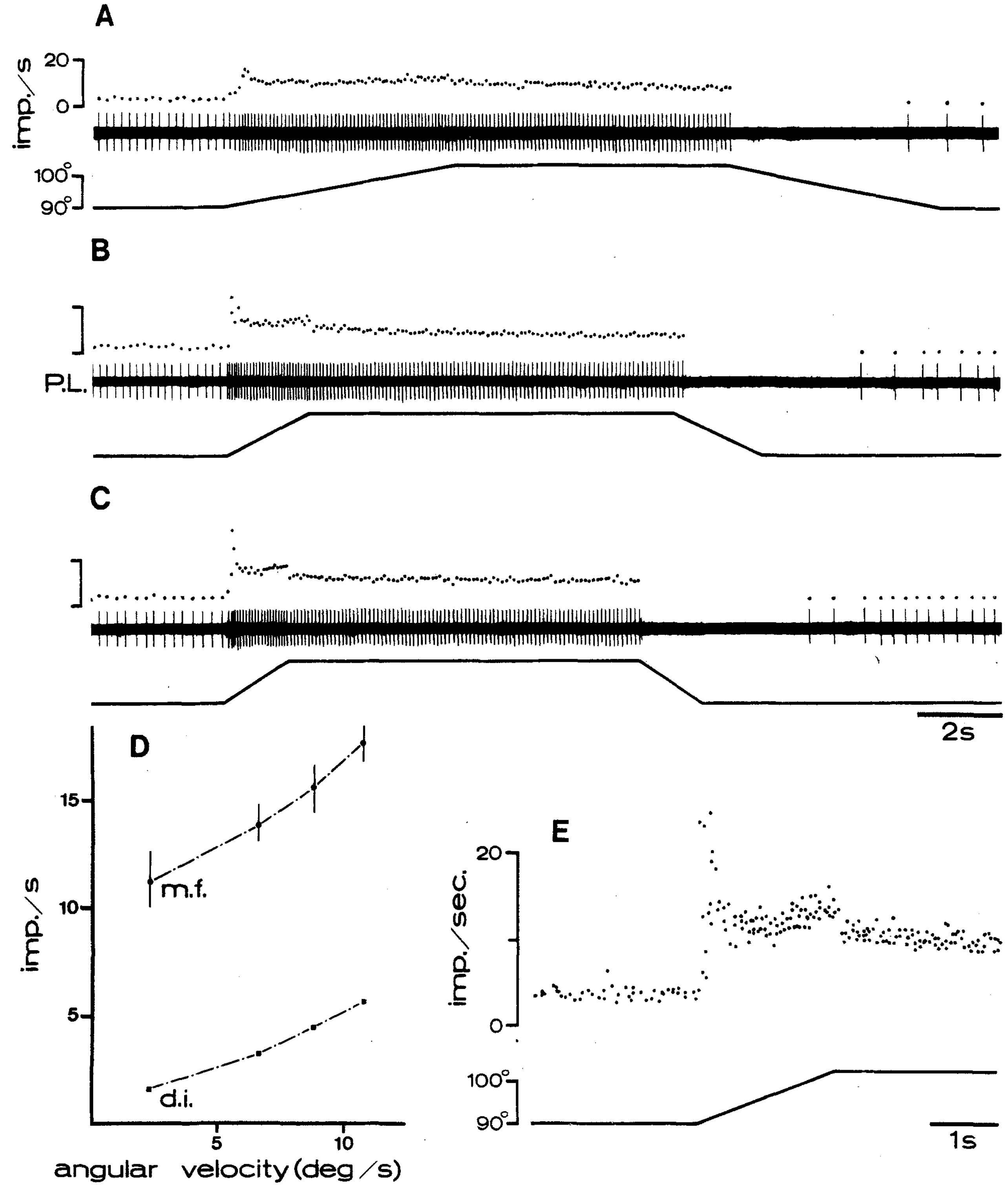

Fig. 5A–E. Characteristics of the primary ending responses to ankle joint movements imposed at constant velocity. **A–C** Responses of a primary ending in Tibialis anterior to ankle joint plantar flexion and dorsiflexion imposed at three different velocities: **A** 2.3 deg/s, **B** 6.6 deg/s, **C** 8.7 deg/s. **D** Comparative analysis of the dynamic sensitivity of the primary ending by its dynamic index (d.i.) and mean frequency (m.f.) curves. Mean frequency was measured by averaging the afferent discharge frequency from the end of the initial burst to the end of the movement. For each value the vertical bars indicate the minimal and maximal instantaneous frequency during analysis. **E** Control of the stability and of the reproducibility of the primary ending response to passive ankle joint movement by the frequencygram method, i.e., superimposition of the primary ending responses (instantaneous frequency) on three identical ankle joint plantar flexions

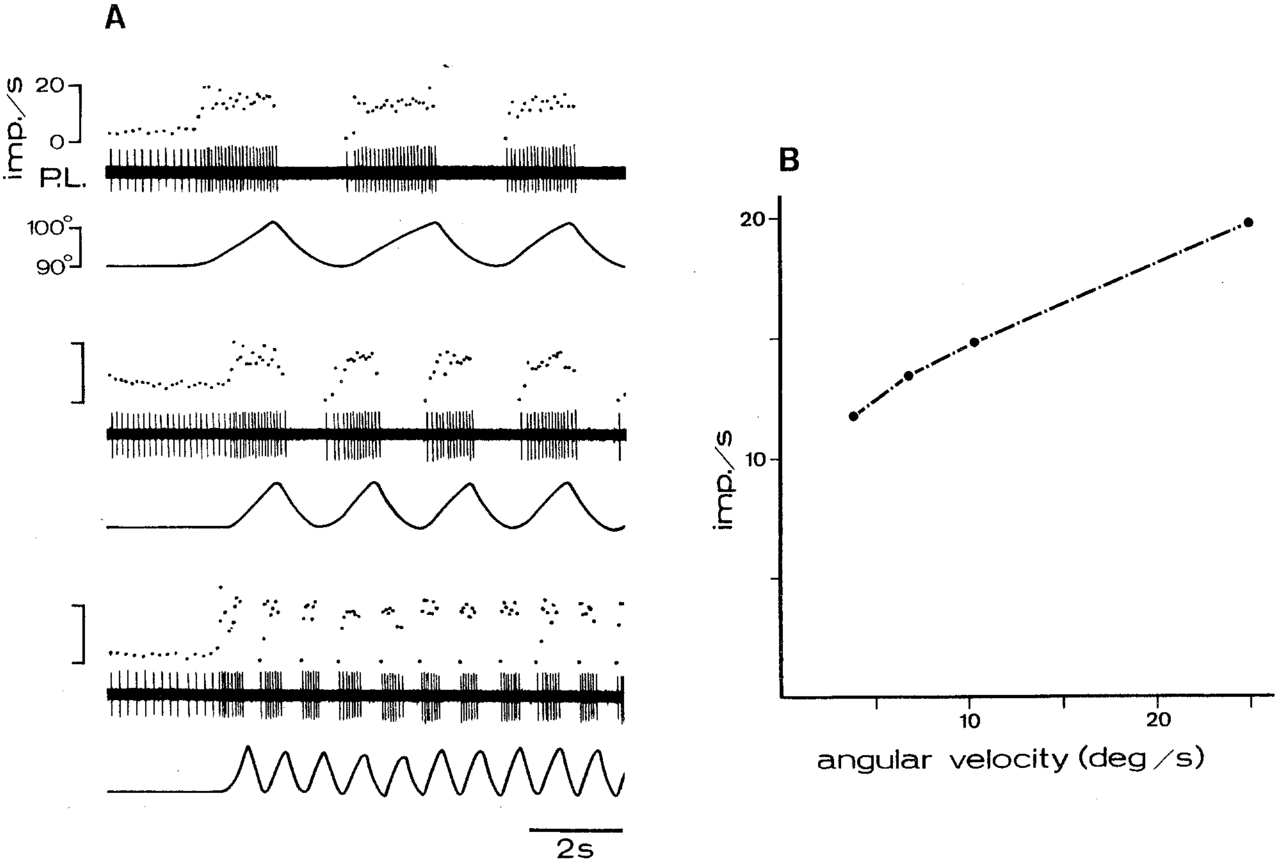

Fig. 6. **A** Primary ending response (TA) to alternate plantar flexion/dorsiflexion movements imposed at different velocities. Passive joint movements were imposed manually. **B** Analysis of the primary ending dynamic sensitivity to alternate movements by the mean frequency curve. Mean frequency (ordinate) was averaged from the primary responses to ten successive joint movements. Angular velocities plotted on abscissa correspond for each point to the mean velocity of ten successive plantar flexion phases corresponding to the ten averaged primary ending discharges

TA and EDL fired spontaneously (2–10 Hz), the impulse periods being more or less variable from one ending to another. From the 90° angle position, 10°–12° movements were passively imposed on the ankle at constant velocities. Two movement patterns were used:

maintained angle position – plantar flexion – maintained angle position – dorsiflexion – maintained angle position (Fig. 5A–C). In these conditions the movement velocity was limited from 1 to 12 degrees per second,

sawtooth-like movements imposing alternatively repeated plantar flexions and dorsiflexions without maintained positions (Fig. 6A–C). Movement velocities up to 25 degrees per second were imposed in these conditions.

The stability and the reproducibility of the sensory responses were estimated by the frequencygram method, i.e., by superposing several spindle afferent responses to the same ankle movement imposed several times (Fig. 5E).

Constant velocity plantar flexion, stretching TA and EDL induced primary ending responses qualitatively almost similar to those observed in the animal when muscle stretches were directly applied to the disinserted tendon. At the onset of the joint movement a short initial burst occurred whose maximal frequency depended on the velocity of the movement (Fig. 5A–C). At the end of the initial burst, primary ending discharge abruptly decreased, then the instantaneous frequency slightly increased up to the end of the joint movement. At the end of the movement their activity progressively stabilized, their discharge frequency depending on the new maintained angle position.

According to Brown et al. (1965), the sensitivity of the primary endings to movement velocity was evaluated by the dynamic index (d.i. curve in Fig. 5D). Considering that after the initial burst the primary ending activity slightly increased during the movement, an attempt was also made to estimate the dynamic sensitivity by measuring the mean frequency

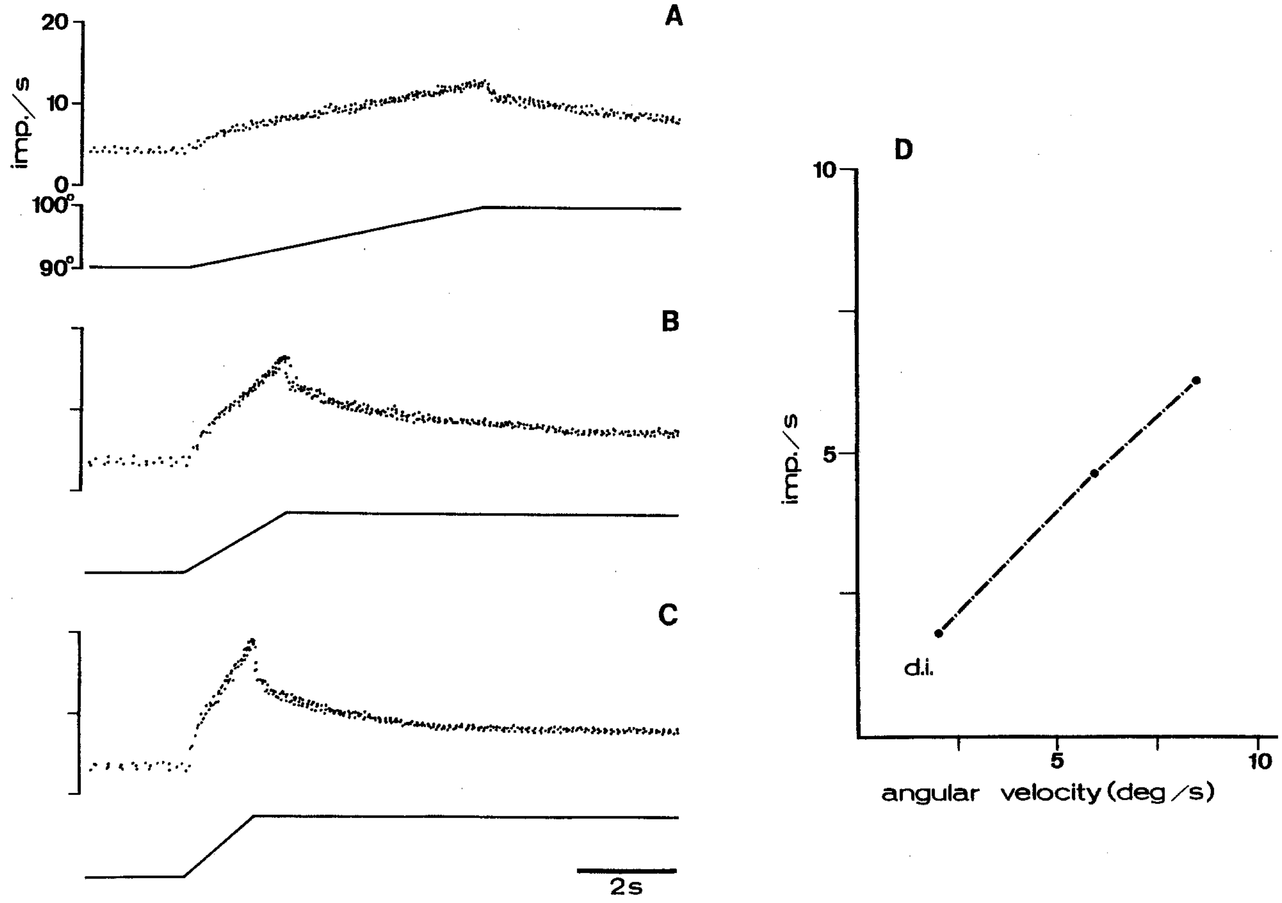

Fig. 7A–D. Secondary ending (TA) responses to ankle joint plantar flexion imposed at different constant velocities. **A** 2 deg/s, **B** 6 deg/s, **C** 8.5 deg/s. Spindle activity is represented in frequencygram form: i.e., in each sequence the responses (instantaneous frequency) of the secondary ending to three identical ankle joint movement were superimposed. The curve **D** illustrates the dynamic sensitivity of the secondary ending measured by the dynamic index (ordinate) of their responses to plantar flexion imposed at different velocities (abscissa)

during the joint movement. In Figure 5D the mean frequency curve (m.f.) has been plotted in parallel with the dynamic index curve (d.i.), both corresponding to the unit illustrated in recordings A, B, and C. The two curves show similar relationships with the movement velocity demonstrating that the mean frequency can also be related to this movement parameter. In the mean frequency curve the vertical bars indicate, for each point, the minimal and maximal values of the discharge frequency during the movement. Mean frequency was always calculated excluding the initial burst.

At the onset of the dorsiflexion (starting position: 100°) the primary ending immediately stopped firing. The silent period duration was apparently more dependent on the amplitude of the joint movement that on its velocity. Primary ending responses to sawtooth-like movements were also characterized by a slightly increasing discharge frequency during the plantar flexion phase. Mean frequency curves calculated by averaging the sensory responses to several movement cycles also showed a relationship with movement velocity (Fig. 6B).

Most of the time when the ankle was maintained at a 90° angle, the secondary endings fired spontaneously. Their tonic activity level was quite similar to that of the primary endings but their inter-spike period was generally much more regular.

TA and EDL secondary ending responses to ankle plantar flexion imposed at constant velocities from 90° were qualitatively different from those of the primary endings. Secondary endings never started firing by an initial burst at the movement onset and their discharge continuously increased along the position change. Moreover, the increasing rate of their instantaneous frequency appeared closely related to the movement velocity as was their maximal frequency at the end of the movement (Fig. 7A–C). Quantitatively, the dynamic sensitivity of some secondary endings, evaluated by the dynamic index curves, did not differ strongly from that of the primary endings (Fig. 7D).

When the ankle movement stopped the secondary ending discharge decreased more progressively than did that of the primary ending, reaching a level depending on the new joint angle position. During a dorsiflexion imposed from 100°, most of the secondary endings stopped firing. Their silent period began at the onset of the movement when they were imposed at the higher velocities used in experiments. During low velocity movements (less than 5° per second) their discharge only decreased progressively and sometimes stopped during the dorsiflexion.

Comparative Study of Muscle Spindle Sensory Ending Responses to Passive and Active Ankle Movements

With a view to confirming the eventual primary role in kinaesthesia of proprioceptive activity from stretched muscle during joint movement, it was necessary to determine whether the spindle afferent patterns differed when the ankle was moved passively and actively. Starting from a maintained 95° position, passive plantar flexion – maintained angle position – passive dorsiflexion were successively imposed on the ankle (Fig. 8A). One minute later the subject was asked to reproduce the same sequence actively. No significant differences were observed in the discharge of the primary and secondary endings in the two situations. Their responses to muscle stretch induced by plantar flexion and their responses to a maintained extended position did not differ strongly, either quantitatively or qualitatively, in active and passive conditions (Fig. 8A, B).

The main differences in the afferent patterns were observed when comparing the sensory ending responses to active and passive muscle shortening. From a 95° starting position, dorsiflexion – maintained angle position – plantar flexion were first imposed passively, then reproduced actively by the subject (Fig. 8C, D). As has been previously described, passive dorsiflexion stopped the discharge of all the primary endings (Fig. 8C) and of some secondary endings. The silence persisted during maintainance of the flexed position, its duration being variable from one sensory ending to another.

During active dorsiflexion, implying an isotonic contraction of the receptor bearing muscle, the afferent discharge of all primary endings stopped or decreased (Fig. 8D). During the isometric contraction maintaining the position reached at the end of the movement, 25% of the primary endings stopped firing while the discharge frequency of the other 75% increased (Fig. 8D). In these conditions their tonic activity could be three or four times higher than during the starting position and their instantaneous frequency was characterized by great variability of the inter-spike periods.

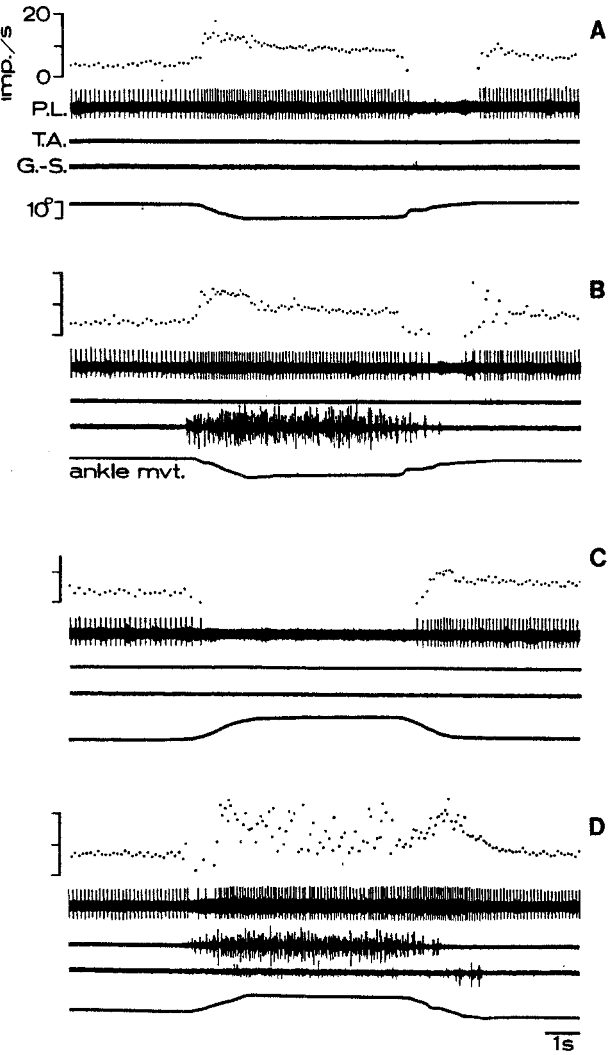

Fig. 8A–D. Primary ending activity during passive and active ankle joint movements. Traces are, from above: instantanenous frequency, afferent unitary potentials, tibialis anterior and gastrocnemius-soleus EMG, ankle joint movement (zero angle position: 95°). **A, B** Primary ending responses to passive (**A**) and active (**B**) ankle joint plantar flexion. **C, D** Responses of the same primary ending to passive (**C**) and active (**D**) ankle joint dorsiflexion

It should be noted that the force produced during isotonic and isometric contractions was always weak, all voluntary movements being performed without load.

Secondary endings could have similar discharge patterns to those of the primary endings during active dorsiflexion and active maintained position, but it was also observed that the activity of some of them could be facilitated during isotonic as well as during isometric contractions. This facilitation sometimes persisted for several minutes after the muscle relaxed, i.e., when the ankle was returned to its initial position.

Discussion

The first set of results presented here reveals the existence of a quantitative relationship between the frequency of the mechanical vibration applied to the tendon of a muscle and the subjective velocity of the illusory movement perceived by the subject during this stimulation.

Considering the microneurography data, it can be suggested that in our experimental conditions, sensations of movement could be mainly induced by an almost selective activation of the muscle spindles. Moreover, the origin of the illusory movement from the primary endings seems to be confirmed by comparison of the characteristics of the vibratory patterns with the response modalities of these receptors to real joint movements.

On the whole, the results suggest that proprioception in the muscles stretched during a joint movement is largely involved in kinaesthesia.

Muscle Afferent Activities Induced by Tendon Vibration

The great sensitivity of muscle spindle afferents to vibratory stimuli has been largely demonstrated in animals (Echlin and Fessard 1938; Bianconi and Van der Meulen 1963; Brown et al. 1967; Matthews and Stein 1969) and more recently in man (Burke et al. 1976).

For primary endings, our microneurography results confirm those of Burke et al. (1976, 1978a, b). These receptors appear, in our experimental conditions, as most sensitive to mechanical vibration applied to the tendon. According to the sensory ending recorded and the vibratory frequency used, the afferent discharge can be driven in an harmonic or sub-harmonic manner. It has to be noted that in spite of these two possibilities of primary ending response, a constant vibration frequency is always related to an almost constant frequency afferent discharge. Compared with the observation of Burke et al. (1976), the main difference observed in our experimental conditions concerns the selectivity of the vibratory stimulus.

Using small amplitude vibrations (0.2–0.5 mm) favours recruitment of very few secondary endings and preferential activation of afferents from the vibrated muscle. Nevertheless, such vibration applied to the elbow muscles was sufficient to induce good sensation of movement and sustained reflex activity (Roll et al. 1980).

These results confirm the observations of Goodwin et al. (1972) suggesting that the illusory movements induced by vibratory stimulation mainly originate from muscle spindle primary endings.

Concerning the slowly adapting pressure receptors, they are very sensitive to vibration applied directly over them but none were strongly activated by vibration applied to the muscle tendon. So their contribution to sensation of movements and motor activity resulting from tendon stimulation appears unlikely.

Relationship Between Vibratory Stimulus Parameters and Sensation of Movement

In all experiments tendon vibration induced illusory movements whose direction corresponds to the direction of a real joint movement stretching the vibrated muscle. Considering that in using small amplitude vibrations it is possible to activate selectively the afferents of the vibrated muscle, it can be suggested that the increased sensory activity induced in this way simulates the proprioceptive discharge occurring during true muscle stretch. The absence of movement sensation consecutive to vibration trains at the same frequency simultaneously applied to the tendons of two antagonistic muscles confirms that the perception of an illusory movement necessitates a prevailing proprioceptive discharge originating from one single muscle. Microneurography data show that this condition occurs systematically during passive joint movement, the afferent activity being always increased during muscle lengthening and decreased or stopped during shortening. During active movement the same discharge pattern is also observed since the afferent activity of the contracting/shortening muscle tends to decrease most of the time. On the contrary the afferent activity is increased most of the time during isometric contraction (Burke et al. 1978b).

Analysis of the illusory movements reproduced by the tracking arm reveals the existence of a relationship between the vibration frequency and the perceived velocity. During muscle vibration the perceived velocity increases with the vibration frequency up to 70–80 Hz, then decreases progressively at higher frequencies. The existence of such an optimal velocity perception could be due either to a decrease of muscle afferent activity consecutive to the occurrence in this frequency range, of sub-harmonic proprioceptive responses to constant vibration frequencies (Hagbarth 1973; Burke et al. 1976), or to saturation of the integrative central structures due to high frequency activity of numerous muscle afferents driven synchronously by tendon vibration.

Comparison of the velocity/frequency curves in Figs. 2 and 3 shows that during alternate stimulation of the antagonistic muscles, the velocity of the illusory movement perceived by the subject was three times greater than the velocity perceived during the vibration of a single muscle. This difference can be explained by the addition of two effects: first, the velocity of the illusory movement induced by the vibration train imposed on one muscle, and second, the post effect occurring at the end of the previous vibratory train applied to the other muscle, and consisting of a reversal of illusory sensation, i.e., an illusory movement in the same direction as that perceived during the vibration train being actually applied.

It has to be noted that in all experiments the illusory movements always appear to be rather slow, not exceeding 15 degrees per second during alternate stimulation.

The fact that a vibratory train at constant frequency induces an illusory movement at almost constant velocity and that this velocity depends on the vibration frequency suggests that the muscle afferents are able to encode this movement parameter. This frequency/velocity relationship was not observed by Juta et al. (1979), probably owing to their experimental conditions which combined different perceptual tasks and motor activities capable of modifying the perception of the illusory movements. According to Clark et al. (1979), the velocity of the illusory movement is also related to the amplitude of the tendon vibration. This relationship could be explained by a rising number of recruited muscle afferents when the vibration amplitude is increased.

Muscle Spindle Responses to Joint Movement

The aim of the microneurography study of the muscle spindle discharge was to determine whether the muscle afferents were able to encode the joint movement parameters.

First of all, it was observed that, qualitatively, the primary and secondary ending responses to muscle stretch or release driven by joint rotation are similar to the responses observed in the animal when muscle length changes were imposed acting directly on the disinserted tendon. The main difference revealed by comparison between animal and human experiments concerns the rate of activity of the spindle afferents, which appears much lower in man. This observation is in complete agreement with those of other authors, notably Vallbö (1974) and Burke et al. (1978a). In the same way we also agree with the results of Vallbö (1974), showing that during maintained joint position "the afferent discharge from secondaries was in most respects very similar to that of the primaries".

Meanwhile, the responses of these two types of sensory ending to passive muscle stretch are very different. Secondary endings never start firing with an initial burst as do the primary endings, and during joint movement at constant velocity the secondary ending discharge frequency increases progressively while the primary endings fire with an almost constant frequency for the whole movement duration.

In this way it may be suggested that during movement the primary ending activity is mainly related to velocity while secondary ending discharge may be a function of both velocity and joint angle position.

The maximal discharge frequency of the secondary endings at the end of movement and the mean frequency of the primary ending discharge averaged along the movement duration both appear closely related to the joint movement velocity as are their dynamic indices.

The characteristics of the primary ending response to constant velocity joint movement and muscle vibration, and the illusory movement perceived at constant velocity during constant frequency tendon stimulation, suggest the ability of muscle spindles to encode this movement parameter.

The comparison of muscle spindle discharge during active and passive movements shows that the proprioceptive message originating from the stretched muscle is the most stereotyped, suggesting that the afferents of this muscle are the most likely to encode joint rotation parameters and so contribute to kinaesthesia. The similarity of spindle responses to both active and passive muscle stretch seems to demonstrate that, during voluntary joint movements carried out at low velocity and without load, the lengthened muscle is free of any fusimotor activation.

In the contracting muscle, the coactivation of alpha and fusimotor neurones seems able most of the time to accelerate the spindle discharge during isometric contraction (Burke et al. 1978b), but, as has been previously demonstrated in animals (Prochazka et al. 1979) and Man (Burke et al. 1978a), the fusimotor effects appear insufficient to maintain spindle activity in the shortening muscle during voluntary movement.

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