Propriomuscular coding of kinaesthetic sensation

Experimental approach and mathematical modelling

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Abstract. The role of propriomuscular information in kinaesthetic sensation was studied. Experiments were carried out on human subjects in whom kinaesthetic illusions were induced by applying tendon vibration with a variable frequency. Six patterns of frequency modulation were used, four of which had an arbitrary form and the other two mimicked natural Ia discharges. The results show that the shape of the illusory movements recorded depended on the type of vibratory pattern used. A mathematical model for the propriomuscular information decoding process is proposed. It takes into account both the agonist and antagonist muscle spindle populations as sources of kinaesthetic information and is based on the assumption that position and velocity information are additively combined. The experimental data show a good fit with the theoretical data obtained by means of model simulation, thus validating our initial hypothesis. Various aspects of the experimental results and the hypotheses involved in the model are discussed.

Introduction

In Man, awareness of body positions and movements involves on the one hand the production of specific information provided by peripheral sensors and on the other hand, the existence of central mechanisms for processing this sensory information. In the present study, we investigated the relationships between the messages arising from muscular proprioceptive receptors and the features of the associated kinaesthetic sensations.

In fact, muscular proprioception plays a predominant role in the conscious perception of body positions and movements. This idea, which was first put forward by Sherrington (1990), is now a well-established fact (Matthews 1982). Propriomuscular information is pro-

duced in muscles by the primary and secondary endings of muscle spindles. Other types of information can also intervene in kinaesthesia, such as visual, tactile or articular cues, but these can be naturally or experimentally neutralized without abolishing movement and position awareness. A decisive argument confirming the role of muscular proprioception has been provided by experimental studies on the kinaesthetic illusions induced by tendon vibration. In fact, the activity of muscle spindle endings can be triggered by high frequency tendon taps, and furthermore, it has been established that tendon vibration is capable of producing conscious sensations of movement or errors in the perceived position of the various body segments (Eklund 1972; Goodwin et al. 1972; Bonnet et al. 1973; Roll and Vedel 1982; Roll et al. 1989). These illusory movements are always such that if an actual movement had taken place, it would have resulted in a lengthening of the muscle the tendon of which was vibrated. It has been demonstrated that these illusions arise mainly from the primary endings of the muscle spindles activated by tendon vibration. Microneurographic studies on Humans (Burke et al. 1976a, b; Roll and Vedel 1982; Roll et al. 1989) have shown that primary endings respond to a one-to-one manner to vibratory stimulation applied to a tendon of the parent muscle. This synchronized activity can be observed up to 70–80 Hz, beyond which limit the primary endings generally produce sub-harmonic frequency responses. Unlike the primary endings, the secondary endings are only slightly sensitive to vibration (Roll et al. 1989). On the other hand, illusory movements can be induced by weak electrical nerve stimulation recruiting only Ia afferent fibers (Gandevia 1985). These results confirm the data by Goodwin et al. (1972) suggesting that the illusory movements induced by vibratory stimulation mainly originate from muscle spindle primary endings. Since the investigations by Eklund (1972) and Goodwin et al. (1972), numerous studies using vibratory stimulation have enlarged our knowledge about the role of muscle spindles in kinaesthesia. The illusory movement velocity has been found for example, to depend on the vibration frequency,

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since the velocity increases with the frequency up to 80 Hz; beyond that frequency level, the velocity decreases and the illusion then vanishes (Roll and Vedel 1982; Sittig et al. 1987; Jones 1988). This decreasing relationship between velocity and frequencies higher than 80 Hz is presumably attributable to the sub-harmonic spindle responses (Hagbarth 1973; Burke et al. 1976; Roll and Vedel 1982; Roll et al. 1989).

Meanwhile, although it is now certain that muscular proprioception plays a preeminent role in kinaesthesia, numerous questions still remain to be answered as to the type of information encoded by muscle spindles and the nature of the central decoding process giving rise to kinaesthetic sensations. These two complementary aspects (coding and decoding) are closely linked and need to be approached in a combined study. As far as the peripheral encoding is concerned, recordings of Ia and II fiber activity in Humans and animals have shown the richness and complexity of the spindle messages. They combine information on both position and velocity in signals which, in addition, depend on the efferent activities of α, β or γ fibers (Crowe and Matthews 1964; Hulliger 1984; Emonet-Denand et al. 1985; Ribot et al. 1986). In the present paper, experimental results are presented along with a mathematical model dealing with the relationships between propriomuscular messages and the related kinaesthetic sensations. The experimental paradigm used to study these relationships involved vibratory tendon stimulation. We recorded and analyzed the illusions of movement evoked in human subjects as the result of the artificial muscle spindle messages induced by frequency-modulated vibration. In the present study, we attempted to test whether frequency-modulated vibration is able to induce illusory sensations of movement, and if so, whether the characteristics of the perceived movement may be correlated with the organization of the vibration frequency modulation. Establishing relationships of this kind between afferent messages and the corresponding perceptual responses was assumed to constitute a possible method of studying the central process whereby the propriomuscular afferent messages are decoded. In the experiments described below, vibratory stimuli were applied alternately to Triceps b. and Biceps b. distal tendons, in order to induce alternate sensations of forearm flexion and extension. The frequency of the vibratory stimulation was modulated in order to reproduce the frequency of natural Ia fiber discharges, such as those recorded during actual sinusoidal or ramp movements (Roll et al. 1989). Furthermore, in order to facilitate the interpretation of the results, we defined a series of arbitrary vibratory patterns with simpler configurations than those mentioned above. We describe the illusory movements resulting from these patterns of tendon stimulation, and propose a mathematical model for the process whereby the muscle spindle information is decoded. This model was an initial attempt at mathematically formulating the central decoding of the afferent spindle messages giving rise to kinaesthetic sensations. It is based on the hypothesis that the decoding process is the converse of the peripheral coding process. The latter was taken to be a simple relation in which the muscle length and changes in muscle length are expressed in a form of a weighted sum, taking into account the adaptive properties of the spindle endings. The responses recorded in human subjects are compared with those obtained with the model, since both responses were elicited by similar afferent patterns.

Methods

Experiments were carried out on a group of 11 healthy human subjects consisting of 6 women and 5 men aged between 21 and 43, all of whom were right handed. At each experimental session, the subject was comfortably seated in an armchair. The left forearm was immobilized and vibrated, lying prone on a horizontal support so that the forearm was at an angle of 90° to the upper arm. The right arm rested on a similar support, except that it was mobile in the horizontal plane and could easily rotate around the elbow axis so that the subject could actively flex or extend his or her right forearm. The movements of the right tracking forearm were recorded.

Vibratory stimulation

Mechanical stimulation was applied by means of two electromagnetic vibrators (Ling Dynamics System, model 101) equipped with Teflon percussion heads. The vibrators were fixed on the bracket supporting the left arm and adjusted at the beginning of the experimental session in such a manner that their heads were applied perpendicularly to the distal tendons of the Biceps b. and Triceps b. Whatever the frequency, all the tendon taps were delivered with a constant amplitude, and their duration was determined by a 4 ms square pulse. The amplitude of each vibration was adjusted at the very beginning of the experiment in order to elicit approximately similar sensations of flexion and extension using a constant 80 Hz vibratory stimulus. During the experimental session, the two muscles were alternately stimulated, each for 4 s, so that when one muscle was vibrated the other was not. Each stimulation sequence lasted for 56 s and was composed of 7 periods of alternating flexor and extensor muscle vibration (Fig. 1).

Vibratory patterns

The intervals between tendon taps were variable and were chosen so as to form a pattern. These intervals were defined as multiples of a 1 ms basic period. The vibrators were driven by a computer using sequential files of interval values, one file for each pattern. The pattern chosen for a sequence was the same with each of the two muscles. Three pairs of patterns were defined, one mimicking the transducing properties of human muscle spindles, and the others arbitrarily chosen. Figure 2 shows the various pattern in the form of instantaneous frequency curves. The maximum frequency used was approximately 83 Hz. The two "spindle like" patterns mimicked the Ia discharges produced
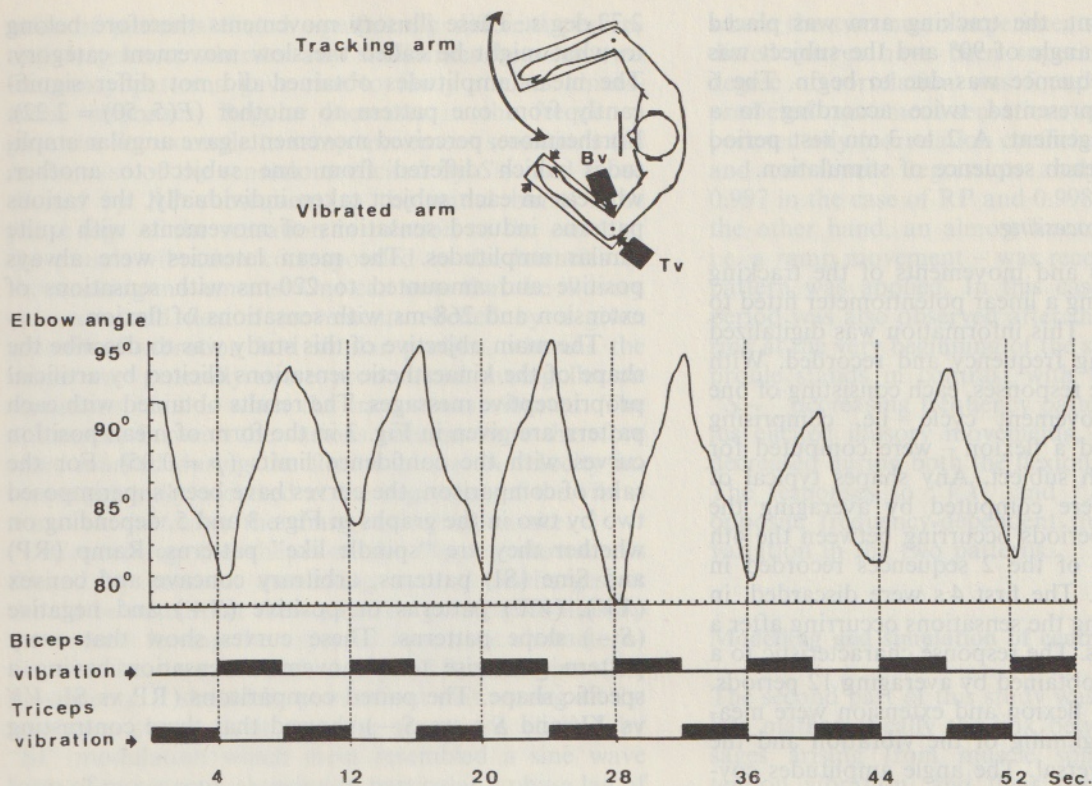
Fig. 1. The upper diagram shows the experimental setup used to induce and record illusory movements. The distal tendons of Biceps b and Triceps b of the left arm were stimulated by vibrators (Bv and Tv, respectively). The movements perceived were reproduced with the right forearm. The lower part gives an example of a tracking movement recorded together with the corresponding sequence of biceps and triceps vibration (lower traces)
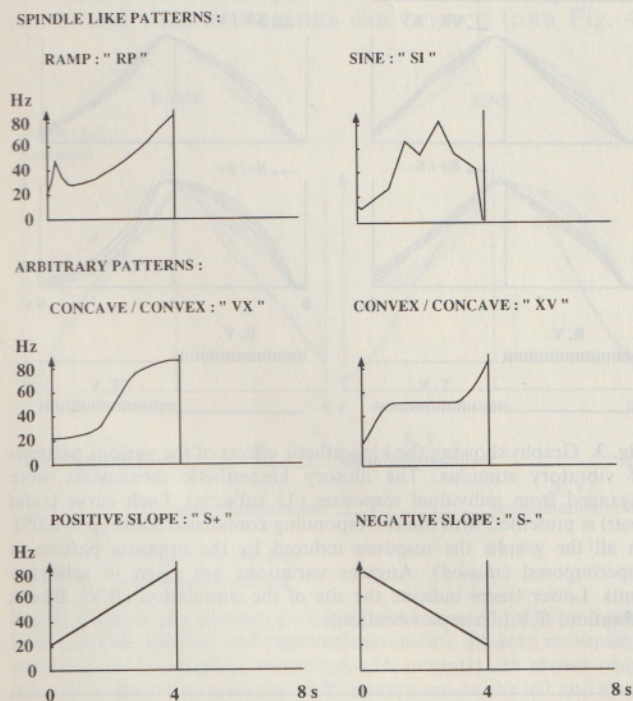

Fig. 2. Frequencygrams of the various patterns used to modulate the vibratory stimuli. The duration of each pattern was 4 s. The silent phase occurring between the 4th and 8th s corresponds to the time during which the antagonist muscle was subjected to this stimulation

either by a constant velocity ramp movement, or by a sine movement. These patterns have been named "RP" and "SI" respectively: they were based on microneurographic recordings in man of the primary ending discharges elicited by ramp (RP) and sine (SI) stretching movements. Two of the 4 arbitrary patterns were characterized by both high and low rates of frequency increase, giving frequency curves with either a convex or a concave shape; the "VX" pattern was composed of a concave shape prior to a convex one and "XV" was organized in the reverse order. The other pair showed linear frequency variations, with a positive slope in the case of "S+" ranging from 20 to 83 Hz, and with a negative slope in the case of "S−" ranging from 83 to 20 Hz. All these pairs of frequency patterns were therefore symmetrical and highly contrasted, so as to facilitate the making of paired comparisons as to the sensations elicited in the subjects by these patterns.

Experimental procedures

The subjected was asked to relax and keep his or her eyes closed throughout the series of experiments, and was then requested to reproduce simultaneously with the right forearm the illusory movement perceived in the vibrated arm. The subject was trained to perform this tracking task during 2 or 3 rehearsals with a vibratory stimulus at a constant frequency of 80-Hz.

Before each experiment, the tracking arm was placed with the elbow at an angle of 90° and the subject was informed when the sequence was due to begin. The 6 patterns were each presented twice according to a pseudo random arrangement. A 2 to 3 mn rest period was introduced after each sequence of stimulation.

Data recording and processing

The angular positions and movements of the tracking arm were recorded using a linear potentiometer fitted to the right support axis. This information was digitalized with a 50-Hz sampling frequency and recorded. With this data base, average responses, each consisting of one complete illusory movement cycle – i.e. comprising both an extension and a flexion – were computed for each pattern and each subject. Any shapes typical of illusory movement were computed by averaging the successive 8-seconds periods occurring between the 4th and the 52nd second of the 2 sequences recorded in response to a pattern. The first 4 s were discarded, in order to avoid including the sensations occurring after a state of motionlessness. The response characteristic to a pattern was therefore obtained by averaging 12 periods. The mean latencies of flexion and extension were measured between the beginning of the vibration and the time of movement reversal. The angle amplitudes covered were also evaluated from the difference between the extreme angular flexion and extension positions measured on the mean curves. The angles covered were subjected to a one way (6 patterns) analysis of variance. Statistics were established for the whole group of subjects concerning the kinaesthetic sensations induced by the various patterns. On account of differences observed in the amplitudes, the mean individual responses were normalized before averaging, and each of the successive values was transformed into a percentage between 0% (lowest) and 100% (highest angle recorded), thus preserving the shape of each. The resulting curves are therefore presented in arbitrary units.

Experimental results

Frequency-modulated tendon vibration elicited sensations of movement in all the subjects, whatever the patterns of modulation used. The sensation was always one of forearm flexion when the triceps was stimulated, and conversely, a sensation of extension was elicited by biceps stimulation. The statistical characteristics of these responses, the means, and the standard deviations of the angular range covered are summarized in Table 1.

The mean amplitude of the illusory movements computed from the whole set of subjects' responses was 10.9 degrees, corresponding to an angular velocity of

2.72 deg/s. These illusory movements therefore belong to what might be called the slow movement category. The mean amplitudes obtained did not differ significantly from one pattern to another ($F(5, 50) = 2.22$). Furthermore, perceived movements gave angular amplitudes which differed from one subject to another, whereas in each subject taken individually, the various patterns induced sensations of movements with quite similar amplitudes. The mean latencies were always positive and amounted to 220-ms with sensations of extension and 268-ms with sensations of flexion.

The main objective of this study was to describe the shape of the kinaesthetic sensations elicited by artificial proprioceptive messages. The results obtained with each pattern are given in Fig. 3 in the form of mean position curves with the confidence limits ($p = 0.05$). For the sake of comparison, the curves have been superimposed two by two in the graphs in Figs. 3 and 5, depending on whether they are "spindle like" patterns, Ramp (RP) and Sine (SI) patterns, arbitrary concave and convex (XV), (VX) patterns or positive $(S+)$ and negative $(S-)$ slope patterns. These curves show that every pattern gave rise to a movement sensation having a specific shape. The paired comparisons (RP vs SI, VX vs XV and $S+$ vs $S-$) showed that these contrasting
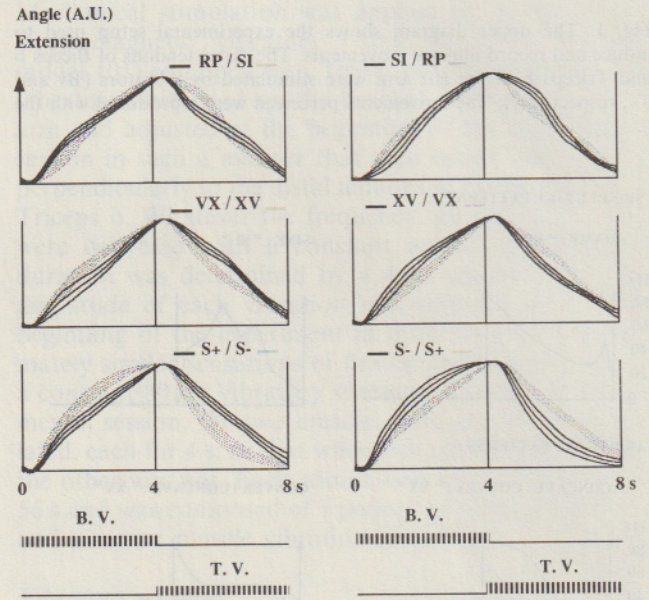

Fig. 3. Graphs showing the kinaesthetic effects of the various patterns of vibratory stimulus. The illusory kinaesthetic movements were averaged from individual responses (11 subjects). Each curve (*solid lines*) is presented with the corresponding confidence limits ($p = 0.05$). In all the graphs the response induced by the opposite pattern is superimposed (*shaded*). Angular variations are given in arbitrary units. Lower traces indicate the site of the stimulation (B.V.: Biceps vibration, T.V.: Triceps vibration)

Table 1. Mean values of the angular amplitude of illusory movements induced by the various patterns of vibratory stimulus (11 subjects). Angles are given in degrees			RP	SI	*VX*	*XV*	*S +*	*S −*
Angles (deg)	Mean		10,87	9,91	11	10,39	11,18	12,01
	S.D.		4,73	4,66	5,42	5,79	5,97	6,93

pairs of patterns elicited significantly different perceptual responses; whereas any similarities between two frequency patterns gave rise to fairly similar kinaesthetic responses. Regular increases in the frequency gave rise for example to ramp movement sensations (as in the case of the sensations elicited by $S+$ and those elicited by RP subsequent to the initial burst). The phase lags of the sensation in relation to the onset of the muscle vibration corresponded to the latencies of the tracking movements. One can note that the illusory extension and flexion movements elicited by a given pattern of vibration had similar profiles, whereas the shape was generally more pronounced during flexion sensations, that is when the triceps was vibrated. The differences between the various patterns were therefore more marked during the flexion phase. A velocity increase generally occurred at the beginning of the vibration – i.e. just after the change of vibration site.

Concerning the shape of the illusory movements elicited by patterns mimicking natural discharges, it should be noted that these patterns gave rise to illusory movements having the expected kinematic characteristics, in the case of both ramp (RP) and sine (SI) movements. It should be pointed out that among all the responses observed, it was the sensations elicited by "SI" modulation which most resembled a sine wave form of movement, showing in particular a phase lag of approximately 90° in the velocity. In the case of the RP pattern, an almost linear position signal was associated with an almost constant velocity curve, except at the very beginning of the movement.

The similarity between the predicted kinematics and the experimental data on the constant velocity movements and since movements can be seen from Fig. 4,
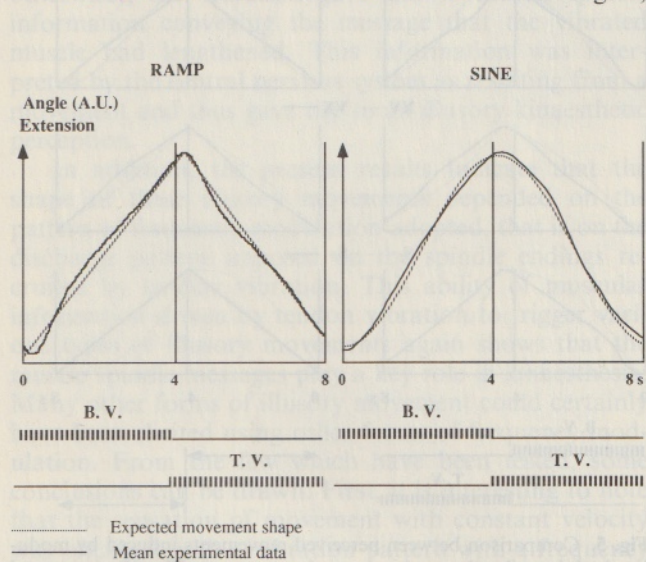
where the two mean experimental curves and the predicted curves have been superimposed. A significant degree of correlation was found to exist between the predicted movement sensations and those recorded experimentally (correlation coefficient r obtained by linear and curvilinear regression analysis were respectively 0.997 in the case of RP and 0.998 in the case of SI). On the other hand, an almost linear illusory movement – i.e. a ramp movement – was recorded when the "$S+$" pattern was applied. In this case, a constant velocity period was also observed after the velocity peak occurring at the very beginning of the stimulation. This linear profile stands in contrast with that produced by the "$S-$" decreasing frequency pattern. The "$S-$" stimulus elicited illusory movements, the velocity of which decreased during both the flexion and extension phases. The responses to "VX" and "XV" patterns showed opposite frequency-dependent fluctuations due to the variation in the two patterns.

Modelling and simulation of central decoding process

The second part of this study was an attempt to formulate mathematically the link between the afferent messages arising from muscle spindles in response to tendon vibration, and their perceptual consequences. This model for the decoding process was elaborated analytically, on the basis of the characteristics of peripheral movement coding. The coding process can be considered at various levels:

– at the elementary coding level achieved by every encoding unit – i.e. muscle spindle endings;
– at the whole population level, taking the whole set of afferent fibers originating in one group of synergistic muscles;
– at the joint level, with messages arising from both the agonist and antagonist muscle groups (in the simple case of a joint having one degree of freedom).

At the most elementary level, numerous studies have contributed to building up a detailed picture of muscle spindle ending activities in Man and in animals (Matthews 1972; Hulliger 1984). One of the major conclusions of these studies was that spindle ending discharges exhibit both static and dynamic sensitivity to muscle length variations. In other words, the signals emitted by muscle spindles contain information about both the position and the velocity of the position changes made by the joint. The possibility that the acceleration parameter is also encoded here can be ruled out for at least one reason, which is that the initial fiber activity occurring at the onset of the ramp stretching pattern is not constantly present (Matthews 1972; Hunt and Ottoson 1976; Burke et al. 1976a, b; Roll and Vedel 1982).

At the muscular level, this signal containing both velocity and position information is produced simultaneously by a set of spindles which have been thought to number 320 and 520 in the Human Biceps b. and Triceps b., respectively (Matthews 1972). One can assume that

Fig. 4. Comparison between perceived movements induced by modulated tendon vibration and expected movements. Illusory movements averaged from individual recordings (11 subjects) are shown (*solid lines*): those obtained with the "RP" pattern are on the left and those obtained with "SI" are on the right. Predicted responses (*gray lines*) are superimposed on the experimental lines, i.e. straight line or sine wave in the case of RP and SI, respectively. The site of the stimulation is indicated on the lower traces (B.V.: Biceps vibration, T.V.: Triceps vibration)

relevant afferent information results each time from the sum of the unitary activities constituting a global afferent flow which is organized on both a spatial and a temporal recruitment basis. This notion of global activity has been introduced into the present model. Furthermore it was assumed that sensations of joint movement are centrally elaborated on the basis of information arising from all the muscles involved in the joint movement. This central convergence hypothesis has been put forward in previous studies. Feldman and Latash (1982), in a model where motor and perceptual aspects have been combined, have proposed the idea that a reciprocal action occurs at the "Position Sense Level", between signals arising from agonist and antagonist muscle receptors. These authors suggest that these afferent inflows may act reciprocally upon a sensory central structure, the incoming signal from the extensor being negative. Based on considerations about spindle discharges, Burgess et al. (1982) formulated a very similar proposition, involving what they called an "opponent frequency code". This idea of a central processing where agonist and antagonist information may be combined is in agreement with experimental results showing that accurate kinaesthetic perception can occur only if both agonist and antagonist afferent information is present (Gandevia et al. 1983). Furthermore, it has been established that during simultaneous tendon vibration of flexor and extensor muscles, the direction and the velocity of the illusory movements elicited depend on the difference between the frequencies of the vibration applied to each muscle (Gilhodes et al. 1986). Equation (1) below expresses this antagonistic relationship.

These considerations led to the following propositions:

1) The peripheral encoding of elbow movement and position involves two antagonistic groups of muscle spindle endings, each providing information about the muscle length together with its rate of variation. The activity of the sets of afferent fibers arising from extensor and flexor will be called Ae and Af, respectively.

2) These signals are processed at each time t, in order to obtain intermediate information such as:

$$R_t = Af_t - Ae_t \qquad (1)$$

(where R_t is assumed to be either positive or negative to simplify the formalism).

3) The relation linking the resulting signal R_t, coding joint positions and movements, and a value θ_t taken to be representative of the associated kinaesthetic sensation, is assumed to be expressible by a linear function. This function, which involves the two variables R_t, θ_t and their first derivatives, is as follows:

$$\theta_t = C_1 R_t + C_2 \, dR_t/dt + C_3 \, d\theta_t/dt + C_4 \qquad (2)$$

(C_1, C_2, C_3, C_4 are constants)

The term dR_t/dt has been introduced in order to account, at the level of the population as a whole, for the discharge frequency adaptation phenomenon (spontaneous frequency decrease with time) observed in Ia fiber discharges. This phenomenon is particularly conspicu-

ous with ramp-and-hold stretching stimuli, at the beginning and after the completion of the stretching phase.

Simulations

In order to compare the model with the subjects responses, i.e. the theoretical vs experimental data, θ_t was computed by means of Eqs. (1) and (2) where Ae and Af are variations analogous to those used for subject stimulation, that is, different patterns of tendon vibration. Due to numerical computation requirements, every pattern was converted into a series of discrete values with constant steps at 20-ms intervals. The pattern tested was then applied alternately to Ae and Af. When either of the afferent channels was active, the other had a null level of activity, in line with the pause in the spindle activity which accompanies passive muscle shortening. Differential equation (2) was solved numerically by means of the Runge-Kutta algorithm. The calculation was carried out taking an initial angular position (θ_{t0}) of 90°. The same set of values was used for constants C_1, C_2, C_3 and C_4, with all the patterns tested. They were chosen in order to give an angular joint amplitude of approximately 10°.

The computed movements presented in Fig. 5 (Theoretical Data) show characteristics which are quite similar to those obtained experimentally with human
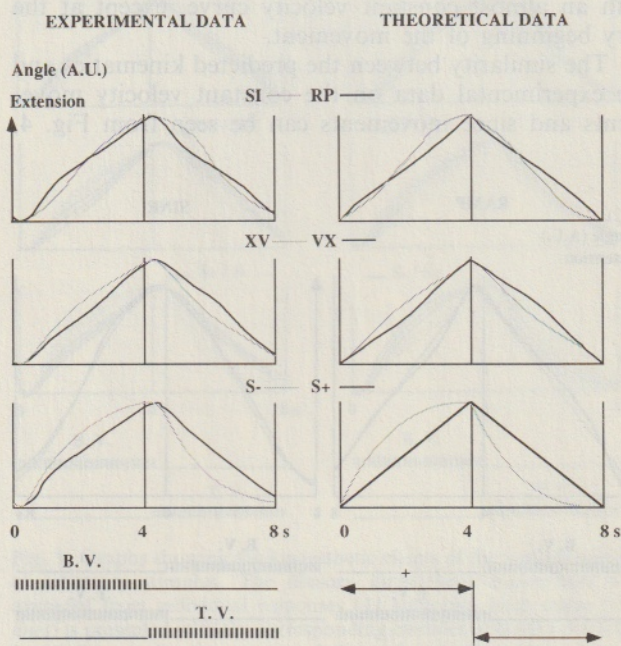

Fig. 5. Comparison between perceived movements induced by modulated tendon vibration and computed movements. The "Experimental data" on the left are the mean kinaesthetic illusions averaged from individual responses (11 subjects). The "Theoretical data" on the right are the responses calculated by means of the mathematical model. In all the graphs two curves are superimposed (solid and gray lines): each pair corresponds to a couple of patterns. Angular variations are given in arbitrary units. The site of the stimulation is indicated on the lower traces (B.V.: Biceps vibration, T.V.: Triceps vibration) on the left, and the sign + or − allotted to the pattern before computation on the right

subjects. Only the following two differences are noticeable: on the one hand the phase lag between the stimulus and responses, and on the other hand, the velocity enhancement occurring in the subjects' responses after the change of variation site. First, the absence of a phase lag in the computed responses was obviously due to the fact that neither the information transmission time nor the duration of the information processing, nor the time needed to perform the tracking movement were taken into account in the model. Secondly the velocity enhancement in the subjects' responses may be attributable to vibratory post-effects. Apart from these slight differences, the similarities in shape between the experimental and theoretical curves, together with the neurobiological arguments mentioned above, confirm that the present model accurately simulated the propriomuscular information decoding process.

Discussion

The general characteristics of the kinaesthetic illusions elicited in the present experiments by frequency-modulated vibratory stimulation were very similar to those observed at the constant frequencies used in earlier studies (Goodwin et al. 1972; Eklund 1972; Roll et al. 1980; Roll and Vedel 1982; Gilhodes et al. 1986). Both constant and modulated vibrations induce a sensation of movement, the direction of which depends on which muscle is vibrated. In the case of the elbow joint, illusory flexion or extension movements can be induced by vibrating the Triceps b. or Biceps b., respectively. In all cases, whatever the stimulus used (modulated or otherwise), the vibration gave rise to muscle spindle information conveying the message that the vibrated muscle had lengthened. This information was interpreted by the central nervous system as resulting from a movement and thus gave rise to an illusory kinaesthetic perception.

In addition, the present results indicate that the shape of these illusory movements depended on the pattern of frequency modulation adopted, that is on the discharge pattern imposed on the spindle endings recruited by tendon vibration. This ability of muscular information driven by tendon vibration to trigger various types of illusory movements again shows that the muscle spindle messages play a key role in kinaesthesia. Many other forms of illusory movement could certainly have been elicited using other forms of frequency modulation. From the few which have been tested, some conclusions can be drawn. First, it is interesting to note that the sensation of movement with constant velocity was obtained with a vibration pattern with a frequency which increased at a constant rate ("$S+$" pattern). On the other hand, the movement perceived by the subjects showed a decreasing pattern of velocity when the frequency of the stimulus applied decreased at a constant but negative rate ("$S-$" pattern). The pattern "$S+$" with a regularly increasing frequency might therefore be thought to code progressive changes of position rather than constant velocity, but this interpretation was not corroborated by the responses observed when the decreasing frequency pattern was applied. Actually, in the context of a position coding hypothesis, a decreasing afferent signal frequency would have been associated with a shortening of the vibrated muscle, giving rise to a sensation of movement in the opposite direction to that observed experimentally. These findings can be taken as evidence supporting the idea that muscular proprioception from both antagonistic muscles is involved in the coding of movement velocity.

The patterns mimicking natural Ia discharges also elicited sensations of movement which were not rigorously similar to natural ramp or sine wave movements. These differences might indicate that the sensory discharge used as a model stimulus was not fully representative of those normally produced on average by spindle ending populations. From this point of view, one can assume that the pattern "$S+$" constitutes a better statistical approximation of natural messages than the pattern "RP" for coding movements with a constant velocity.

The vibration patterns which gave frequency curves moving in opposite directions (XV and VX) gave rise to illusory perceptions of movement the velocities of which were also opposed. This finding again clearly shows that the frequency structure of the proprioceptive inputs is one of the main factors determining the characteristics of illusory movements.

Among the general characteristics of these illusory movements, one in particular is worth pointing out, namely the fact that these movements showed quite low velocities. In fact, the illusory movements recorded were no faster than a few degrees/second, whether constant frequency (Goodwin et al. 1972; Roll et al. 1980, 1982; Sittig et al. 1987), or modulated frequency stimulation was used. There are at least two ways of interpreting this fact: first, the role of muscle spindles may be naturally limited to the encoding of slow movements, i.e. those which are generally thought to operate under feedback control (closed-loop regulation mode), unlike the ballistic movements which are performed in the "open-loop" mode. The second argument is based on the idea that the tendon vibration method of activating the Ia sensory channel may have limitations, due in particular to the fact that the vibratory stimulus may synchronize the activity of spindles which are not naturally synchronized (Matthews and Stein 1969). This hypothesis is not in line with the data showing that illusory sensations of very rapid movement can be elicited by applying electrical stimulation to primary afferents, despite the fact that this type of stimulation is known to synchronize the various unitary activities involved (Gandevia 1985). The latter author has established moreover that the velocity of illusory motions increased with the stimulus intensity. These findings indicate that the number of primary afferent fibres recruited may be one of the factors determining the velocity of perceived movements. Apart from this fact, it is possible that the natural proprioceptive input from the non-vibrated antagonist muscle may contribute significantly to decreasing the velocity of the perceived movement (Gilhodes et al. 1986).

The data obtained with the mathematical model are in good agreement with the experimental results. The model in fact accounts for most of the experimental data. This concordance, along with the fact that the model was developed using the latest information available about the movement coding effected by muscle receptors, argues in favour of our working hypotheses, particularly as regards the idea that these proprioceptive inputs may contain summated velocity and position information, and that the information arising concomitantly from agonist and antagonist muscles during a single movement must necessarily be combined at the central level.

The central nervous system may fulfill an afferent information decoding function which is the converse, mathematically speaking, of the sensory coding one. The work of interpreting these messages might involve a process similar to that suggested by Crowe et al. (1980) in connection with the analysis of afferent signals. In the present case, the relation between the lengthening of the muscle and the discharge frequency of the whole set of fibres involved should amount to approximately the weighted sum of the muscle length and its change in length. Various mathematical models have been put forward to account for specific features of spindle behaviour, such as the encoding process carried out by muscle spindles. These models generally took into account both position and velocity variables, setting them either in an additive relationship (Lennerstrand and Thoden, cited in Matthews 1981b) or a multiplicative one (Houk et al. 1981). Houk et al. furthermore suggested that the velocity component may intervene in a power form with a constant exponent. Establishing a general model for muscle activities is very difficult due to the extreme diversity of the contextual situations in which spindle organs are involved: passive vs active and isometric vs isotonic conditions, together with the static and/or dynamic sensitivity modulation exerted by afferent beta and gamma fibers. It is worth noting however that these mathematical descriptions of the spindle behavior were based on unitary spindle data obtained from animal experimentation. This might in fact explain some of the discrepancies between our model and these spindle models, along with the fact that the tendon vibration used in the present study activated a population of muscle spindles which may have had quite specific characteristics and sensitivity. It has been reported however that microstimulation applied to single fibres arising from neuromuscle spindles does not elicit illusory sensations of movement (Macefield et al. 1990). In addition, it is necessary to bear in mind the fact that proprioceptive messages convey information about the length and changes in length of the muscle, whereas kinaesthetic sensations relate to the positions and movements of the limb segment. These sensations are probably built up from convergent sensory inputs of various kinds. This whole set of information might then form a context in the light of which the information arising from the muscles is interpreted.

The last point which requires to be discussed concerns the changes in the static and dynamic sensitivity of spindle receptors, which depend on the gamma fusimotor and beta skeletofusimotor command systems. For the model to function properly taking these spindle sensitivity variations into account, one has to assume that the parameters of Eq. (2) (C1, C2, C3, C4) are also liable to vary and that they depend on the static and dynamic gamma and beta activities. As suggested by Matthews (1981a), this would mean that a copy of these efferent messages is sent to the appropriate nervous structures responsible for the decoding process.

In conclusion, the results of our experiments show that muscle proprioception contributes towards creating sensations of movement with highly specific and varied characteristics. These sensations of movement involve the interpretation of proprioceptive messages arising from both agonist and antagonist muscles, as well as depending on laws governing the receptor discharge frequency level. Lastly, the model for the central decoding of proprioceptive messages proposed here takes into account the velocity and position information which is jointly conveyed to the central processing structures via the muscle proprioceptive sensory pathways.

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