RESEARCH ARTICLE

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Proprioceptive population coding of two-dimensional limb movements in humans: I. Muscle spindle feedback during spatially oriented movements

Abstract The proprioceptive coding of multidirectional ankle joint movements was investigated, focusing in particular on the question as to how accurately the direction of a movement is encoded when all the proprioceptive information from all the muscles involved in the actual movement is taken into account. During ankle movements imposed on human subjects, the activity of 30 muscle spindle afferents originating in the extensor digitorum longus, tibialis anterior, extensor hallucis longus and peroneus lateralis muscles was recorded from the lateral peroneal nerve using the microneurographic technique. In the first part of the study, it was proposed to investigate whether muscle spindle afferents have a preferred direction, as previously found to occur in the case of cortical cells, and to analyze the neural coding of the movement trajectories using a "population vector model." This model is based on the idea that neuronal coding can be analyzed in terms of a series of vectors, each based on specific movement parameters. In the present case, each vector gives the mean contribution of a population of muscle spindle afferents within one directionally tuned muscle. A given population vector points in the "preferred sensory direction" of the muscle to which it corresponds, and its length is the mean frequency of all the afferents within that muscle. Our working hypothesis was that the sum of these weighted vectors points in the same direction as the ongoing movement. The results show that each muscle spindle afferent, and likewise each muscle, has a specific preferred sensory direction, as well as a preferred sensory sector within which it is capable of sending sensory information to the central nervous system. Interestingly, the results also demonstrate that the preferred directions are the same as the directions of vibration-induced illusions. In addition, the results show that the neuronal population vector model describes the multipopulation proprioceptive coding of spatially oriented 2D limb movements, even at the peripheral sensory level, based on the sum vectors calculated from all the muscles involved in the movement. In an accompanying paper, the coding of more complex 2D movements such as those involved in drawing rectilinear and curvilinear geometrical shapes was investigated.

Key words. Proprioception · Muscle afferents · Sensory coding · Spatially oriented movements · Microneurography · Humans

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Introduction

The coding and transmission of information within the nervous system raises questions which have been intriguing neurophysiologists for years. There have been many attempts to find and describe some of the general principles underlying this neural coding.

The population coding (or ensemble coding) theory places the emphasis on the idea that the encoding is performed by a whole neuronal population. For population coding to be possible, it is essential that several receptors should be able to respond to the same stimulus, and also that their individual responses to this stimulus should not be identical. A large number of teleological arguments have been put forward to support the ensemble coding theory. First, a so-called economy argument was developed by authors who pointed out that since each neuron participating in ensemble coding will be able to deal with stimuli of several different kinds (Ray and Doetsch 1990), the potential number of different messages will be much greater than the number of neurons available. Secondly, these authors put forward a reliability argument

according to which a distributed ensemble system will be "of considerable stability and reliability" because it will probably not be seriously affected by the loss of only one or a few neurons (Ray and Doetsch 1990). Lastly, they formulated a stability argument according to which ensemble coding is likely to involve a relatively high signal-to-noise ratio, so that the messages triggered by identical stimuli are likely to be more consistent in this case than when the coding is carried out by individual receptors (Ray and Doetsch 1990).

Although it is generally recognized nowadays that most of the information transmitted within both the central and peripheral nervous systems is encoded and transmitted by large populations of neurons, the question as to how this neural coding is carried out is still a controversial issue. In the case of the sensory system, there exists a continuously growing body of evidence indicating that large populations of sensory neurons transmit even simple peripheral stimuli to the central nervous system. To quote an example, the results from two animal studies on muscle force coding have shown that the sum (Crago et al. 1982) and the mean (Hulliger et al. 1995) of the discharge rates of populations of sequentially recorded Golgi tendon organ afferents correctly coded the total muscle force.

The coding of limb movements has attracted special attention lately. Muscle afferents, especially muscle spindle afferents, are known to play an important role in the coding of limb movements (see for example Roll and Gilhodes 1995; Roll et al. 1996). Quite recently, large populations of muscle spindle afferents were simultaneously recorded from the cat dorsal root, and a method based on the ability of these neural populations to discriminate between sinusoidal muscle stretches of different amplitudes was developed (Johansson et al. 1995a, 1995b). Using this model, Bergenheim and coworkers (Bergenheim et al. 1995, 1996, 1998) established several important points in connection with the population coding of limb movements: first, populations of primary muscle spindle afferents discriminated more accurately than single afferents between muscle stretches of different amplitudes (Bergenheim et al. 1995). Secondly, mixed populations of primary and secondary muscle spindle afferents and Golgi tendon organ afferents discriminated between muscle stretches of different amplitudes better than populations consisting of a single type of afferents (Bergenheim et al. 1996).

In the case of humans, Ribot-Ciscar and Roll (1998) carried the idea of population coding even further by establishing that the information about joint movements is encoded by muscle spindle afferents originating in antagonist muscle groups (see for example Roll et al. 1995; Ribot-Ciscar and Roll 1998) and, furthermore, that the encoding is probably carried out by afferents from all the muscles involved (in terms of lengthening or shortening) in the movement. The authors described this multi-muscle population coding as a "sensory landscape" depicting the joint movement (Roll and Gilhodes 1995). In a recent study, this hypothesis gained further support (Verschueren et al. 1998), since the effects of vibrating synergistic wrist muscle tendons showed that movement perception is probably based on information arising from all the synergistic muscles.

In all the studies mentioned above, population coding was investigated at the sensory level. A few studies have also focused, however, on population coding at other levels of the nervous system. Using the so-called "neuronal population vector" model, Georgopoulos et al. (1984), for example, have shown that populations of motor cortical cells can predict the direction of a forthcoming movement. This approach was based on the idea that many cells, such as motor cortical cells, may show a particularly high level of activity during movements performed in a specific direction. This direction has been called the cell's "preferred direction." The preferred direction of each activated cell along with the activity of that cell during a given movement yields a population vector, the direction of which is almost exactly that of the actual movement.

While it would possibly be expected, from the known properties of spindle afferent activity reflecting muscle length and velocity and the mechanical actions of muscles on the skeleton (Mussa-Ivaldi 1988; Sanger 1994), that the direction of movement is coded in the complete set of proprioceptive data, this has not yet been demonstrated empirically. In the present study, it was proposed to investigate the population coding of ankle joint movements in various directions, focusing in particular on the question as to how accurately the direction of a movement can be encoded on the basis of all the muscle spindle information arising from all the muscles undergoing deformation during the performance of the actual movement. In an accompanying paper, the population coding of more complex 2D movements such as rectilinear and curvilinear geometrical shapes will be investigated.

Materials and methods

Experimental setup and microneurographic recordings

The experiments were conducted on 11 healthy subjects between 22 and 28 years of age. All the subjects gave their informed consent to the experimental procedure as required by the Helsinki Declaration. The study was approved by the local ethics committee. Single muscle spindle afferents originating from the tibialis anterior (TA), extensor digitorum longus (EDL), extensor hallucis longus (EHL) and peroneus lateralis (PL) muscles were sequentially recorded at the level of the lateral peroneal nerve using the microneurographic technique (see, e.g., Vallbo and Hagbarth 1968; Bergenheim et al. 1999).

The subjects were comfortably seated in an armchair, with their legs positioned in cushioned grooves so that a standardized relaxed position could be maintained throughout the experiment without any muscle activity occurring. The knee joint was at an angle of about 120–130°. The right foot was placed on a stationary pedal. The left foot was attached to a rotating pedal connected to a motor imposing 2D movements on the ankle (see Fig. 1B). Single unit recordings were performed using insulated metal microelectrodes (impedance 500 kΩ to 1 MΩ tested at 1 kHz with a tip diameter of about 5–10 μm). The electrode was inserted percutaneously by hand at the level of the popliteal fossa. The recordings
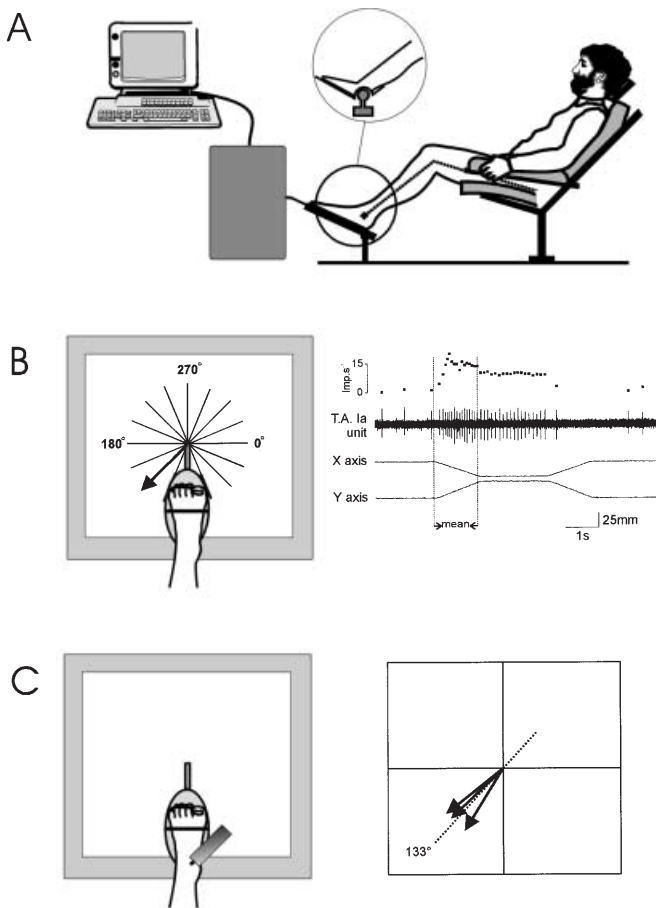
Fig. 1A–C Experimental setup. **A** Position of the subject, the movable pedal and the motor. **B** The 16 test directions. Note that 90° corresponds to a plantar flexion and 270° to a dorsiflexion. *On the right* is a recording from a tibialis anterior primary muscle spindle afferent responding to a 135° movement (as indicated *on the left*). *The diagram at the top* shows the instantaneous frequency of the response, *the middle diagram* shows the original recording and *the lower diagram* shows the *X* and *Y* coordinates of the movement. For the further analyses, the mean frequency discharge during the movement (indicated by *horizontal bars*) was calculated. **C** Application of the vibrator. In this example, the tibialis anterior muscle tendon was vibrated, and the direction of the perceived illusions reported by the subject is indicated *on the right*

were continuously monitored on an oscilloscope and a loudspeaker. Single units were isolated by adjusting the position of the microelectrode in minute steps. The neural activity was amplified using a band pass of 300–3000 Hz to ensure an optimal signal-to-noise ratio.

The afferents were classified as either primary or secondary muscle spindle afferents on the basis of: (1) their dynamic sensitivity to passive muscle stretching, (2) whether or not they were silent during muscle shortening, (3) their responses to small sinusoidal stretches superimposed on a ramp stretch, and (4) their sensitivity to mechanical vibration. The origin of the muscle spindle afferent was determined by manually pressing the tendons of the different muscles. For a more detailed description of the criteria used for classification purposes, see Bergenheim et al. (1999), and for a more detailed discussion see Burke (1997). The absence of muscular activity was controlled throughout the experiments by recording surface EMG activity of the receptor-bearing muscle.

Machine imposing 2D movements

Two-dimensional movements were imposed on the ankle using a machine which was specially designed for this purpose (Rematique, Saint-Etienne). This machine comprises a metal rod, which moves freely and smoothly in a 2D plane, and this movable rod can be freely rotated around its own axis (360°). More precisely, the lower end of the pedal rests on a ball joint (see enlargement in Fig. 1A). As the rod moves in the two-dimensional front plane of the machine, it is allowed to slide under the pedal. This means that an upwards movement on the front plane of the machine (i.e., 270° in Fig. 1B) created a dorsiflexion of the ankle joint. A sideward movement to the left (i.e., 180° in Fig. 1B) resulted in an eversion and not a translation of the foot. It should be noted that although the front plane of the machine is flat, the tip of the foot moved in a single, slightly curved plane in relation to the flat surface of the machine. The center of rotation of the foot was adjusted and lined up with the center of the rotation of the ankle joint.

The movements in the *X* and *Y* planes were computer controlled (PC Pentium Pro, using Labview, National Instruments Corporation). The movements consisted of passive ramp-and-hold movements in 16 different directions (as illustrated in Fig. 3). The movements were run according to a randomized scheme, and their amplitudes measured at the tip of the foot and velocity were constant (25 mm and 38.5 mm/s in the plantar flexion direction). Ninety degrees corresponded to a plantar flexion, 270° to a dorsal flexion, 0° to a movement to the right and 180° to a movement to the left.

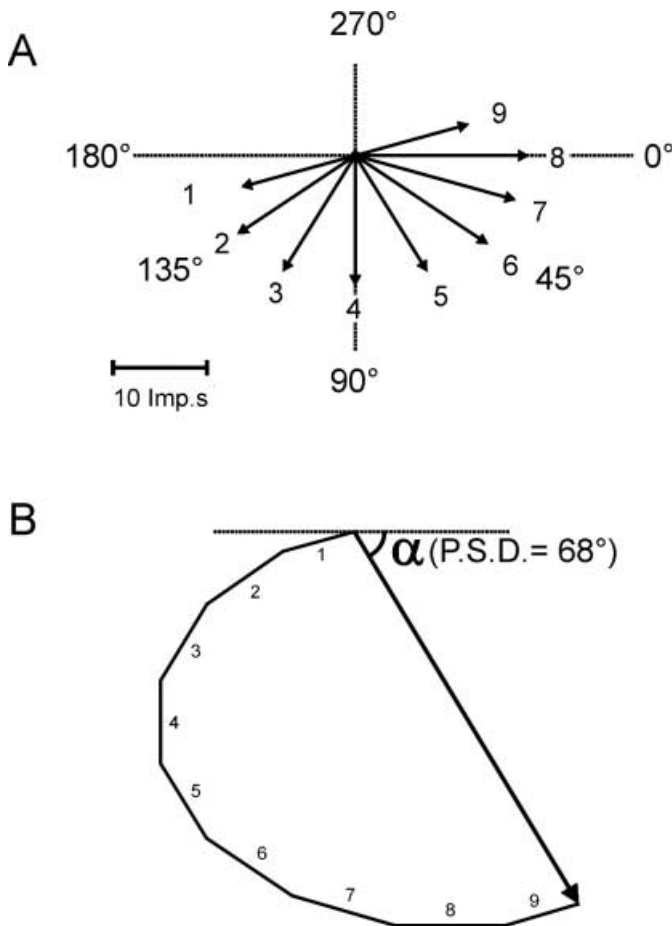## Calculating the preferred sensory direction by means of the microneurographic method

Using the microneurographic data, it was possible to calculate the "preferred sensory direction" of each muscle spindle afferent, as previously described in the literature (see, e.g., Schwartz et al. 1988; Caminiti et al. 1990; Georgopoulos 1990). In the first step, the sensitivity of each afferent to limb movements in the 16 different test directions was established by recording the mean discharge frequency during the "outward" movement in each direction (see Fig. 3). In the second step, this response was denoted by a vector: the direction of this vector corresponded to the direction of the movement, and the length corresponded to the mean discharge frequency recorded during the "outward" phase of this test movement (see Fig. 2A). In the third step, the preferred sensory direction of the unit was taken to be the sum vector of its responses to all 16 directions tested (see Fig. 2B).

The preferred sensory direction of each afferent (given by an angle) was therefore noted. The mean preferred direction of all the afferents within one muscle was then calculated, and the same procedure was applied to each of the four muscles which could be investigated using the microneurographic technique (i.e., the TA, EDL, HL and PL muscles). No clear-cut difference was found to exist between the preferred directions of primary and secondary muscle spindle afferents. The responses of both afferent types were therefore pooled for these calculations.

Calculating the preferred sensory direction by means of the muscle tendon vibration method

There are at least six main muscle groups acting on the ankle joint and transmitting sensory proprioceptive information about joint ankle movements to the brain. For this analysis, it was necessary to include two muscle groups that could not be tested with the microneurographic technique, i.e., the gastrocnemius soleus (GS) and the tibialis posterior (TP) muscles, which meant that the preferred direction of these muscles could not be calculated in the way described above. It was attempted in the present study to overcome this difficulty by inducing kinesthetic illusions by applying muscle tendon vibration (Roll et al. 1995).

The tendon vibration experiments were conducted on ten healthy subjects. The experimental conditions (armchair, subject's posi-

Fig. 2A,B Calculation of preferred sensory direction for each single afferent. **A** The response of an extensor digitorum longus primary muscle spindle afferent to 16 test directions. The length of each vector corresponds to the mean frequency of the response to the movement in that particular direction. **B** Calculation of the sum vector of the vectors from **A**, in order to establish the preferred sensory direction (α). In this case the preferred sensory direction was 68°

tion, etc.) were exactly the same as in the microneurographic experiments (see above). An electromagnetic vibrator (VM 80, Bersac, Colombes) was used to selectively vibrate six left ankle muscle tendons. The muscles vibrated were the TA, EDL, EHL, PL, TP and GS. The vibrators were fixed to a holder, and the vibration was applied perpendicularly to the distal muscle tendons (vibration frequency 80 Hz, peak-to-peak amplitude 0.2 mm). The vibrator was equipped with a changeable head so that heads of different sizes could be used depending on the morphology of the vibrated tendon.

After a vibration period of 10 s, the subjects were asked to indicate the direction of the illusion they perceived on a report sheet, on which only the horizontal and vertical directions were given as indications (see Fig. 1C). Each of the six tendons was vibrated 3 times. Eighteen tests were performed in this way in a randomized order, and the subject indicated all the illusions perceived on the same report sheet. In order to assess the effects of vibrating different tendons, any statistical differences between the perceived illusions were analyzed using the Watson-Williams test.

It was assumed that the direction of the illusions induced by vibrating a single muscle might constitute an indirect index to the preferred sensory direction of that muscle. To test this hypothesis, the directions of the perceived illusions were compared with the preferred directions of the muscles determined by microneurography (i.e., those of the TA, EDL, EHL and PL muscles).

Population vector analysis

In an attempt to investigate the neural population coding of 2D movements, the data recorded by microneurography were analyzed using a "neuronal population vector model" (see, for example, Georgopoulos 1990; Roll and Gilhodes 1995). This model is based on the idea that this neuronal coding can be analyzed in terms of a series of population vectors and by finally calculating a sum vector. In our case, each population vector gives the mean contribution of all the muscle spindle afferents within one directionally tuned muscle. To apply this model it was first necessary to test whether the mean tuning curves (see Fig. 7) of each population of afferents of each muscle were cosine shaped. To this end, a multiple regression analysis was used in order to find the constants b_0, b_1 and b_2 for the tuning equation:

$$F=b_0+b_1 \sin\theta+b_2 \cos\theta$$

where F corresponds to the discharge frequency and θ to the angle (direction) of the tested movement.

A particular population vector points in the preferred sensory direction of a given muscle, and its length corresponds to the mean frequency of the responses of all the afferents within that muscle during a movement in a particular direction. The hypothesis underlying the vector model is that the sum of these weighted muscle vectors (the sum vector) was likely to point in the same direction as the ongoing movement. Any afferents that responded during less than 5% of the total movement performance time were excluded (3 out of 25). The response of each single afferent was normalized by taking its largest response in any direction to be equal to 1. Note that even if there were no difference in preferred directions between primaries and secondaries, they clearly differed in their tuning curves. Therefore, only the responses of the primary afferents were included in the population vector analysis.

The preferred sensory direction used in the calculations was either the mean preferred direction of all the muscle spindle afferents within the muscle, as calculated using the microneurographic method, or the mean angle of the directions of the illusions elicited by applying tendon vibration (see above).

Statistical analysis

Two circular statistical analyses were carried out in this study (Batschelet 1981). The Rayleigh test was used to test the clustering of all the preferred directions in all the units belonging to the same muscle. The *V*-test was performed in order to test: (1) whether the preferred directions calculated by inducing kinesthetic illusions had a tendency to cluster around the preferred directions calculated by microneurography and (2) whether the population vectors had a tendency to point in the direction of the corresponding imposed straight movements.

Results

Each muscle has a preferred sensory direction

A total number of 30 muscle spindle afferents was tested (25 Ia: 7 EDL, 2 PL, 13 TA, 3 EHL; and 5 II: 3 EDL, 1 PL, 1 TA). Figure 3 gives as an example the response of a primary muscle spindle afferent originating from the EDL muscle during ramp and hold movements imposed in 16 different directions. The instantaneous frequency of this unit increased conspicuously in response to several outward movement directions (i.e., movements away from the center of the working space, see Fig. 3) ranging from 337.5° to 135° (in the clockwise direction), and its response varied depending on the direction. The maxi-
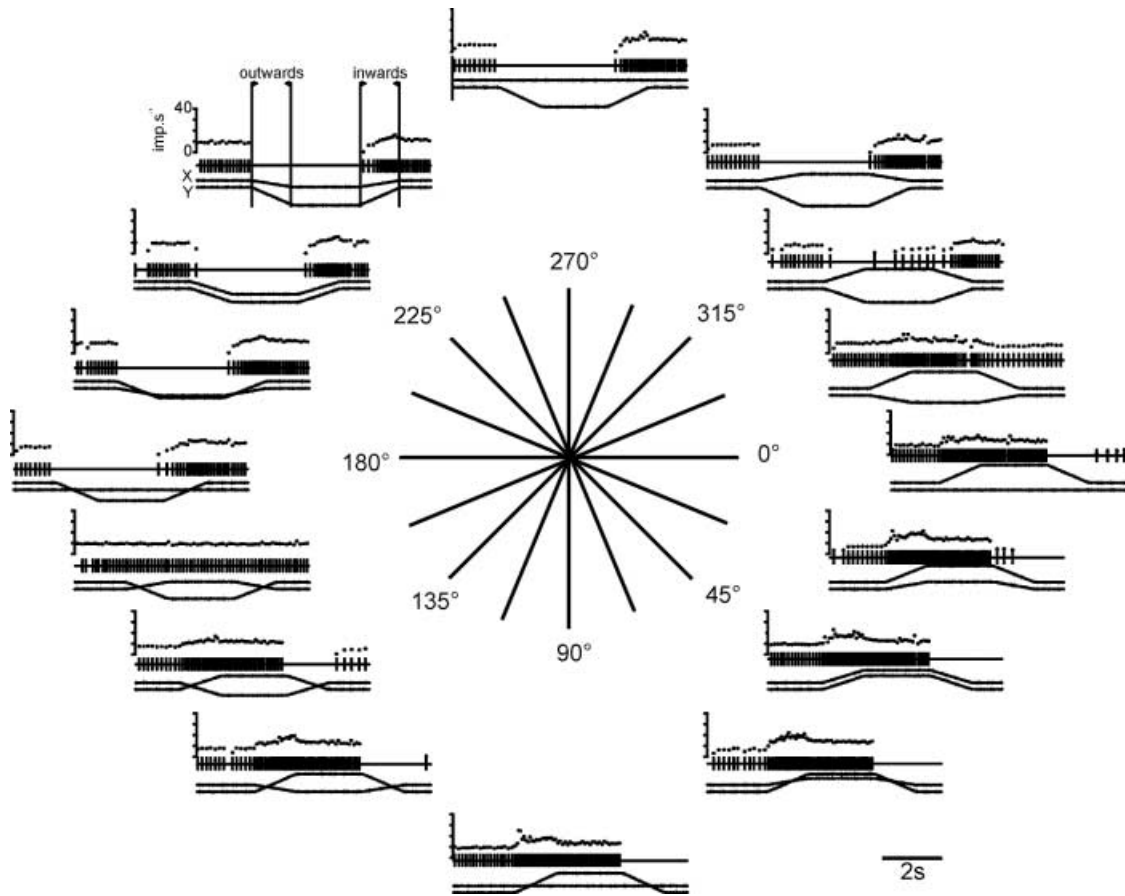
Fig. 3 Example of a recording. This figure illustrates the response of an extensor digitorum longus primary muscle spindle primary afferent to all 16 test directions. In each diagram the instantaneous frequency of the response is given *at the top*, the spike train *in the middle* and the *X* and *Y* coordinates of the movement *at the bottom. The horizontal bars* show the outward and the inward parts of the movements (i.e., working from the center of the working space to the periphery and vice versa)

mum response was observed with the 67.5° movement (90° equals a straight plantar flexion). In the case of the 157.5° movement, this unit showed no change at all in its pattern of activity during the movement, but was always tonically active, and in the case of movement directions ranging between 180° and 315°, it was silent during the outward part of the movement.

During the inward part of the movements (i.e., moving from the periphery to the center of the working space, see Fig. 3), the activity of this unit increased during the return part of the 180° to the 315° movements. It showed no change during the return part of the 157.5° movement, and decreased between the 337.5° and 135° movements.

On the basis of the responses to movements in all 16 directions, the preferred sensory direction of each unit was calculated as described above. The calculated preferred sensory direction of the unit illustrated in Fig. 3 (primary muscle spindle afferent from the EDL muscle) was 68° and its largest response corresponded to the
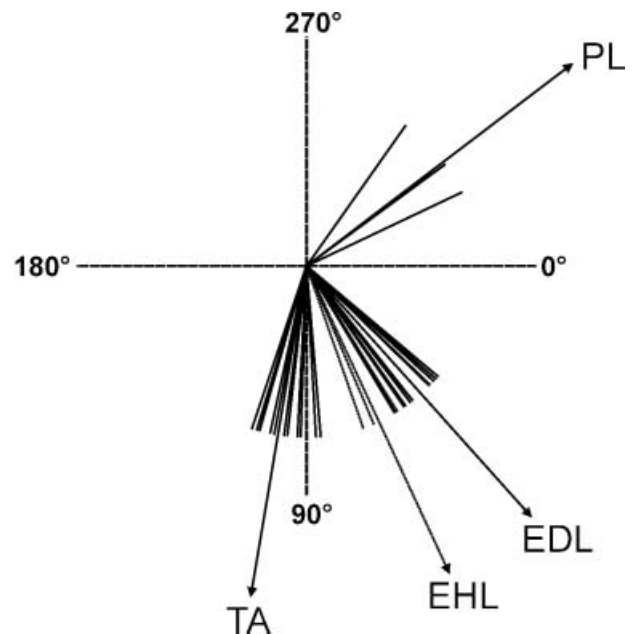
Fig. 4 Calculation of each muscle's mean preferred sensory direction. This figure shows the preferred sensory direction of each afferent tested (*short, fine lines*). *The long, bold lines* illustrate the mean preferred sensory direction of each particular muscle. Note that the data illustrated in this figure involve only the angle of the preferred sensory direction

67.5° direction. The preferred sensory directions of all the units tested were determined and recorded separately depending on the muscle of origin. These directions are given by the short, fine lines in Fig. 4.

As can be seen in this figure, the preferred sensory direction varied from one unit to another, even within the same muscle. The averaged angles obtained on the whole population of units from one muscle yielded the preferred sensory direction of that muscle (long, bold lines). Interestingly, the preferred direction varied between the muscles even when they were close synergists. The fact that there did exist a preferred direction was established statistically in the case of the TA muscle ($r=0.996$, $n=14$, $P<0.001$, Rayleigh test) and the EDL muscle ($r=0.995$, $n=10$, $P<0.001$, Rayleigh test). Since the samples were smaller ($n=3$) in the case of the units from the PL and the EHL muscles, these statistical tests could not be carried out in the case of these muscles.
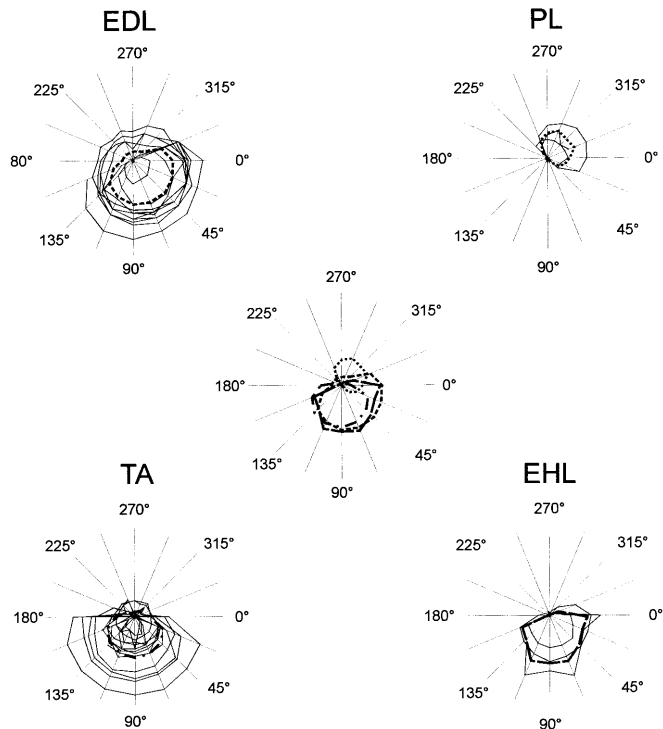
Each muscle has a preferred sensory sector

In fact, as previously mentioned, all the afferents were found to be responsive to several movement directions on both sides of their preferred sensory directions. A "preferred sensory sector" was therefore defined for each unit and then for each muscle. This is illustrated in Fig. 5, where the connected points correspond to the mean discharge frequency of each afferent recorded during the outward part of the movements in each particular direction (thin lines). The bold lines in each diagram give each muscle's average preferred sector.

The units in each of the muscles tested showed a quasi-homogeneous pattern of behavior. In the case of the EDL muscle, for example (upper left diagram), the primary muscle spindle afferents started discharging at an angle of around 158°, and the discharge frequency then increased until the direction nearest to the calculated preferred sensory direction was reached (67.5°), before gradually decreasing at angles of between 67.5° and 338° and becoming completely silent in the case of the remaining directions. The three secondary endings corresponding to this muscle fired in each of the directions tested, but with a variable pattern of frequency.

The middle diagram in Fig. 5 illustrates the preferred sensory sectors of all the muscles tested. It can be observed that these sectors overlapped among the synergist muscles in the anterior part of the leg, although they were not completely superimposed. The preferred sectors were 180–22.5° in the case of the TA, 158–338° in that of the EDL and 0–158° in that of the EHL muscle. On the other hand, the PL muscle, which can be said to be an antagonist with respect to the ankle flexor muscles, was found to have a completely different preferred sensory sector (248–45°).

As can be seen in Fig. 5, there were some angular sectors in which none of the muscles tested responded. It seems likely that the remaining two muscle groups acting on the ankle joint, which could not be tested under


Fig. 5 The preferred sensory sectors of each afferent and the mean preferred sensory sector of each muscle. In this figure, each diagram gives the preferred sensory sector of a muscle. The response of each single afferent in each of the 16 directions has been plotted as a point on the axis of the corresponding movement. The points were then connected by drawing *thin lines*, thus forming a sector which was that afferent's preferred sensory sector. *The bold lines* give the mean preferred sensory sector of all the afferents. *The middle diagram* gives the mean preferred sectors of each of the muscles

our experimental conditions (i.e., the TP and GS muscles), may have responded to the movements in these directions.

In conclusion, the results presented above show that the muscle spindles in a particular muscle are sensitive to movements in several different directions. This range of movement directions, which we have called that muscle's preferred sensory sector, is highly specific to each muscle. Within this preferred sensory sector, the muscle shows maximum sensitivity to a particular movement direction, i.e., the preferred sensory direction, and here again this direction is specific to each muscle.

The direction of the vibration-induced illusions corresponds to the preferred sensory direction of the vibrated muscle

The directions of the perceived illusions elicited by the selectively applied tendon vibration are given in Fig. 6. An example of the results obtained on one subject is given in A, where short, thin lines indicate the movement direction perceived in each trial and the long, bold lines indicate the mean direction perceived in the three trials
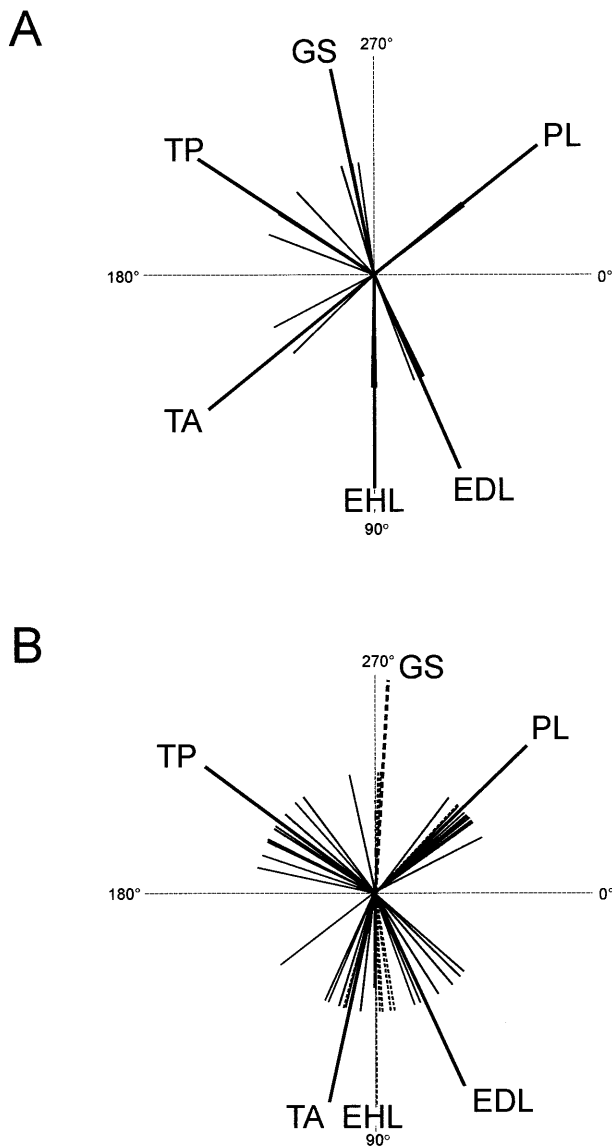
Fig. 6A,B Directions of the vibration-induced illusions of movement. **A** The responses from one subject indicating the directions of the perceived illusions when the tibialis anterior (*TA*), extensor digitorum longus (*EDL*), extensor hallucis longus (*EHL*), peroneus lateralis (*PL*), gastrocnemius-soleus (*GS*) and tibialis posterior (*TP*) muscle tendons were vibrated selectively (*short, fine lines*). Each muscle tendon was vibrated 3 times, and the mean of these three trials was calculated (*bold, long lines*). **B** This diagram gives the results on all the subjects combined. *The short, fine lines* correspond to the mean direction recorded with each muscle and each subject (*n*=10). *The long, bold lines* illustrate the mean direction in all the subjects combined, taking each muscle separately. The directions of the perceived illusions differed significantly (*P*<0.05, Watson-Williams test) between all the muscles
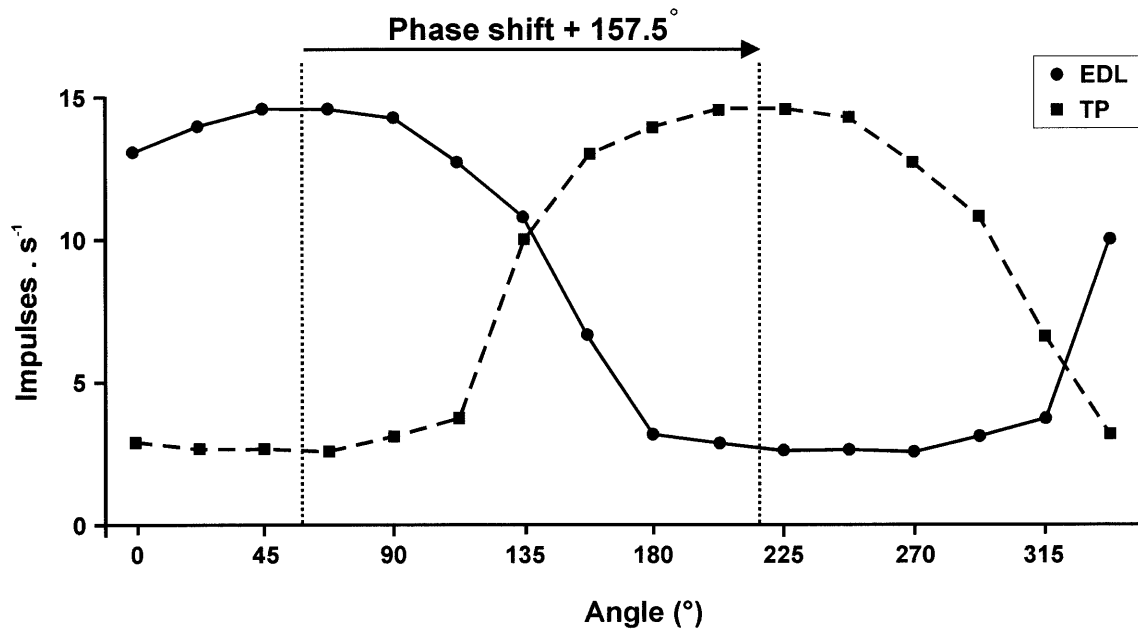
Table 1 Preferred sensory directions of the six main muscle groups acting on the ankle joint (*left-hand column*), as calculated by means of the microneurographic method (*middle column*) and/or by applying selective muscle tendon vibration (*right-hand column*). The values are average values, followed by the SD

Muscle	Microneurography (°)	Vibration (°)
TA	95.8±4.8	102.2±9.5
TP		217.2±9.0
GS		273.6±8.1
PL	311.3±12.2	316.1±4.3
EDL	59.4±5.8	65.2±13.0
EHL	73.0±3.9	89.5±3.6

Figure 6B gives the mean directions of the kinesthetic illusions recorded upon vibrating each muscle in all the subjects combined. The directions of the illusions induced by vibrating each of the six muscles were statistically different (*P*<0.05, Watson-Williams test).

Upon comparing the preferred directions calculated by microneurography with those of the illusions elicited in response to tendon vibration, these two values turned out to be very similar in the case of all the muscles tested. In fact, taking all the muscles combined, these two methods for establishing the preferred sensory direction yielded directions that were clustered (*u*=8.592, *n*=40, *P*<0.0001, *V*-test). Furthermore, when a more detailed analysis was performed, it was observed that even when each muscle was taken separately, the two differently calculated preferred sensory directions were also clustered (TA: *u*=4.30, *n*=10, *P*<0.001; EDL: *u*=4.19, *n*=10, *P*<0.001; PL: *u*=4.42, *n*=10, *P*<0.001; EHL: *u*=4.26, *n*=10, *P*<0.001, *V*-test). All the preferred directions calculated and the directions of the perceived illusions are reported in Table 1. The finding that the preferred directions calculated using the microneurographic method and the directions of the illusions perceived in response to the tendon vibrations did not differ significantly is of great importance, since it indicates that tendon vibration could in fact constitute a valid means of estimating the preferred direction of the TP and the GS muscle afferents that could not be tested using the microneurographic technique.

At this stage, we were therefore able to establish the preferred sensory direction in the case of the muscles that cannot be recorded by microneurography. However, the mean afferent activity occurring during the movements of these unexplored muscles still needs to be determined. For this purpose, it was decided to use a similar method to that previously described by Ribot-Ciscar and Roll (1998), where the responses of two antagonist muscles serve as "templates." The choice of template muscles was based on similarities between the preferred sectors of the illusions occurring in response to vibration. As can be seen in Fig. 6, the illusions corresponding to TP and the EDL muscle vibration showed similar patterns of dispersion, whereas those observed upon vibrating the GS muscle tendon resembled that obtained with the EHL muscle. The response of the TP muscle

in the case of each of the muscles vibrated. First, it can be clearly seen that the illusions perceived differed depending on which muscle was vibrated. Secondly, applying vibration to some tendons (e.g., in the case of the PL muscle) resulted in very clearly oriented illusions, whereas in other cases the results obtained were more widely dispersed (e.g., in the case of the TP muscle).

Fig. 7 Tuning curves in the case of the extensor digitorum longus and the tibialis posterior muscles (*EDL, TP*). The tuning curve of the EDL was calculated on the basis of direct microneurographic recordings. The tuning curve shows the average response of all the muscle spindle afferents from the EDL to all 16 test directions (*X*-axis). The TP tuning curve was modeled on the basis of the EDL tuning curve. In fact, this curve was phase shifted by 157.5°, which corresponds to the differences in the preferred sensory directions based on the effects of muscle tendon vibration (*dotted horizontal bars*). Note the distinctly cosine shaped tuning curve, which confirms the validity of the neuronal population vector model

was therefore modeled based on the response of the EDL muscle, and the response of the GS muscle was based on that of the EHL muscle. In addition, since the preferred directions of the EDL and the EHL muscles and those of the "template" muscles differed, the tuning curves of the "template" muscles were phase shifted +157.5 and –157.5, respectively (see Fig. 7), corresponding to the differences in the preferred directions.

Another important point that emerges from Fig. 7 is the fact that the directional tuning of the afferents was cosine shaped. More precisely, a cosine tuning function was fitted to the data from all four muscles (see "Materials and methods" section). The constants obtained for the fit were the following for the EDL: $b_0=8.26$, $b_1=5.98$, $b_2=3.46$ ($r^2=0.96$), for the EHL: $b_0=7.01$, $b_1=7.95$, $b_2=2.47$ ($r^2=0.93$), for the TA: $b_0=6.48$, $b_1=6.85$, $b_2=-0.71$ ($r^2=0.94$), for the PL: $b_0=3.83$, $b_1=-3.52$, $b_2=3.47$ ($r^2=0.91$).

The neuronal population vector model as a means of describing the proprioceptive coding of oriented limb movements

The neuronal population coding analysis was performed on the basis of a total number of 25 primary muscle spindle afferents (13 TA, 7 EDL, 3 EHL and 2 PL). The sec-
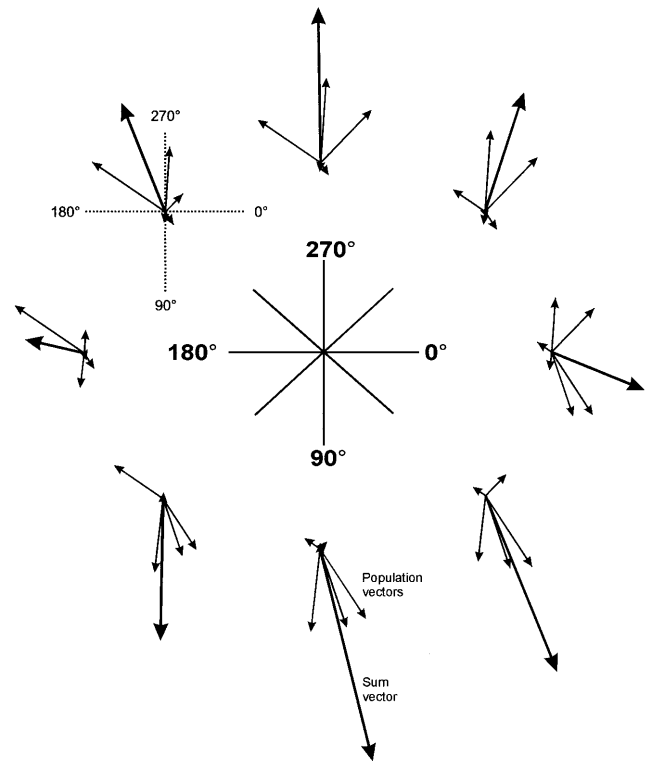
Fig. 8 The neuronal population vector model. This figure gives the results of this attempt to describe the sensory multipopulation coding of 2D spatial limb movements using the neuronal population vector model (eight directions are illustrated). Each diagram gives the result obtained in one movement direction. *The thin lines* correspond to the population vector of each muscle, and *the bold lines* give the sum vector of all six population vectors. *The middle diagram* gives the actual direction of each movement

ondary muscle spindle afferents were not used in this analysis since their sensitivity and response characteristics differed conspicuously from those of the primary afferents.

The results of the vector model analysis of muscle spindle afferent population coding are illustrated in Fig. 8, where the muscle spindle population vector obtained in the case of each muscle is indicated by thin vectors, and the sum vector is illustrated with bold lines (eight of the directions tested are illustrated in separate diagrams). As can be seen from this figure, distinctly different population vectors were obtained in all the directions tested, and these vectors were found upon statistical analysis to point in the actual directions of the ongoing movements (u=4.99, P<0.0001, V-test).

Discussion

Each muscle spindle and each muscle has a preferred sensory direction and a preferred sensory sector

The results presented in this paper indicate that each muscle spindle afferent has a specific preferred sensory direction and also that each muscle itself has a preferred sensory direction, defined here as the average preferred direction of all the muscle spindle afferents belonging to that muscle. This is not surprising since preference of this kind was shown to exist in the motor system as regards force production and motor unit behavior (Herrmann and Flanders 1998). The results show that the preferred sensory direction varies from one unit to another even within the same muscle: these differences probably depend on the location of the muscle spindle receptors within the muscle (Matthews 1972).

The differences observed here between the preferred sensory directions of the various muscle spindles throws interesting light on their ability to participate in population coding. As early as the late 1960s, it was suggested that population coding might require the individual receptors in the population to have a number of specific functional properties. First, the range of sensitivity of individual receptors in the populations would have to differ slightly, i.e., the receptors in the population must not all produce identical temporal or spatial patterns of response to the same stimulus (Erickson 1968). Secondly, the sensitivity tuning of the individual receptors in the population would have to overlap. The present finding that there exist some slight but clear-cut differences between the preferred directions of the various muscle spindle receptors within one muscle and that each receptor will therefore respond differently to a movement in any given direction consequently suggests that here we have conditions which are highly suitable for population coding.

The present data also show that each of the synergist muscles (TA, EDL and EHL) has its own preferred direction and its own preferred sensory sector. This is not surprising, since the anatomical sites at which the tendons are inserted differ considerably between these muscles, as do the paths taken by the tendons under the retinaculum extensorum ligaments. However, as regards the population coding aspects discussed above, the fact that the muscles do show different preferred directions and sectors is of great relevance to their population coding ability, since it may mean that not only the receptors within one muscle, but also receptors belonging to different synergist muscles, might constitute a set of receptors which is highly suitable for population coding.

Is the neuronal population vector model applicable at the peripheral sensory level?

One of the aims of this study was to investigate whether the populations of spindle afferents, with which the various muscles acting on a single joint are equipped, are able to encode spatially oriented movements. If one takes the simultaneously activated afferents in the various muscles, the resulting sum vector will certainly encode the directions of the ongoing movements.

The fact that the sum vectors in Fig. 8 did not always point exactly in the direction of the ongoing movement needs to be discussed. First, errors can be introduced when the fundamental assumptions of the population vector method are not perfectly satisfied (Mussa-Ivaldi 1988; Sanger 1994; Deneve et al. 1999). Indeed, the tuning curves were not exactly cosine and the distribution of the preferred directions was not exactly uniform. The results of applying a multiple linear regression method to our set of data showed that the accuracy of the movement direction determination was about 10% greater than the vector method. The vector population method was nevertheless preferred because it was previously found to be a relevant model for interpreting the direction of complex illusory movements (Roll and Gilhodes 1995; Roll et al. 1996). In our previous experiments, we established that when several muscles were covibrated, the subjects experienced illusory movements, the direction and velocity of which obeyed a vector sum law. Other causes of errors may have been: (1) the small number of PL afferents tested (n=3), which may not have been fully representative of the whole population of PL afferents; (2) it is possible that our attempts to model the activity of the TP and GS muscles may have introduced a small amount of error; and (3) each preferred sensory direction was established by testing the responses of the afferents to movements in various directions in 15° steps: testing the direction in smaller steps might have yielded more accurate preferred sensory directions and thus slightly improved the results. However, testing the directional preferences in more than 16 directions was not really feasible in the present study, mainly due to the time it would have required.

Interestingly, the results obtained here point to the existence of some general sensory coding principles that have previously been found to pertain specifically at the cortical level. In previous studies, a clear-cut correlation has been found to exist between the direction of both two- and three-dimensional arm movements and the neural activity recorded in the motor cortex (Schwartz et al. 1988; Georgopoulos et al. 1984; Georgopoulos 1990;

Scott and Kalaska 1997), the posterior parietal cortex (Kalaska et al. 1983, 1989, see accompanying paper; Kalaska 1991), and the premotor cortex (Caminiti et al. 1990).

It may be worth mentioning that the study by Georgopoulos and coworkers focused on the coding of movements of the tip of the hand in relation to the shoulder, whereas in the present study we investigated the coding of movements of the tip of the foot in relation to the ankle. The latter type of coding can be said to be of a more local type, thus illustrating that motor cortical activity might at least partially reflect this local information (Mussa-Ivaldi 1988; Scott and Kalaska 1997).

In conclusion, it emerges clearly from these results that each muscle is able to send the CNS sensory information relating to a specific range of movement directions, which we have called that muscle's preferred sensory sector. Within this preferred sensory sector, the muscle receptor population shows maximum sensitivity to movements performed in an equally specific direction, which we have called the preferred sensory direction. In addition, even at the early peripheral sensory level, the neuronal population vector model is a means of describing the multipopulation proprioceptive coding of spatially oriented 2D limb movements.

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