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RESEARCH ARTICLE

**Jean-Pierre Roll · Mikael Bergenheim**
**Edith Ribot-Ciscar**

# Proprioceptive population coding of two-dimensional limb movements in humans: II. Muscle-spindle feedback during “drawing-like” movements

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**Abstract** It was proposed to study the proprioceptive sensory coding of movement trajectories during the performance of two-dimensional “drawing-like” movements imposed on the tip of the foot. For this purpose, the activity of the muscle-spindle afferents from the Extensor digitorum longus, Tibialis anterior, Extensor hallucis longus, and Peroneus lateralis muscles was recorded from the lateral peroneal nerve using the microneurographic technique. The drawing movements, describing geometrical shapes such as squares, triangles, ellipses, and circles, were imposed at a constant velocity in both the clockwise and counterclockwise directions. A total number of 44 muscle-spindle afferents were tested, 36 of which were identified as primary and eight as secondary afferents. Whatever the shape of the imposed foot movement, the primary endings from one muscle never discharged throughout the whole trajectory (on average, they discharged for only 49.2% of the length of the trajectory), whereas all the secondary endings discharged for most part of the drawing trajectories (average: 84.8%). The relationship between afferent discharge rate and direction could be described with a cosine-shaped tuning function. The peak of this function corresponded to the preferred sensory direction of the receptor-bearing muscles. The whole path of a given geometrical drawing movement was found to be coded in turn by each of the primary afferents originating from each of the muscles successively stretched. The contribution of each population of muscle afferents from each ankle muscle was represented by a “population vector”, whose orientation was the preferred direction of the muscle under consideration and whose length was the mean instantaneous frequency of the afferent population. The “sum vector” corresponding to the sum of all these weighted “population vectors” was found to point in the instantaneous direction of the drawing trajectory, i.e., the tangent to the trajectory. These findings suggest that trajectory information is already encoded at the peripheral level on the basis of the integrated inputs provided by sets of receptors belonging to all the muscles acting on a given joint.

**Key words** Proprioception · Muscle afferents · Sensory coding · “Drawing-like” trajectories · Microneurography · Humans

## Introduction

After the companion paper by Bergenheim et al. (2000), dealing with the proprioceptive coding of spatially oriented straight movements in two-dimensional (2-D) space, the present paper focuses on more complex 2-D movements, such as those involved in the drawing of rectilinear and curvilinear geometrical shapes.

It has by now become widely recognized that proprioceptive cues constitute an important, reliable source of information about specific movement parameters (Cordo 1990; Gandevia and Burke 1992; Gandevia 1996; Roll et al. 1996). The authors of recent studies on animals and humans have pointed out that, to be able to efficiently encode movement parameters, the central nervous system (CNS) has to monitor the activity of an population of afferents from a given muscle (Bergenheim et al. 1996) and requires both agonist and antagonist inputs to be able to encode accurately the direction and velocity in the case of simple, voluntary, alternating flexion/extension movements (Gilhodes et al. 1986; Ribot-Ciscar and Roll 1998).

Since each of the muscles surrounding a given joint is richly endowed with muscle-spindle receptors, the proprioceptive feedback evoked by even quite simple movements is always generated by the whole set of muscles

J.-P. Roll (✉) · E. Ribot-Ciscar
Laboratoire de Neurobiologie Humaine, UMR 6562,
Université de Provence/CNRS,
Avenue Escadrille Normandie Niemen,
13397 Marseille Cedex 20, France
e-mail: lnh@newsup.univ-mrs.fr
Tel.: +33 4 91 28 82 98, Fax: +33 4 91 28 86 69

Mikael Bergenheim
Department of Musculoskeletal Research,
National Institute for Working Life, Box 7654,
907 13 Umeå, Sweden

undergoing mechanical deformations (lengthening, shortening, contraction, etc.) during a particular movement. The question recently addressed by Gandevia and Burke (1992) as to how many muscles are required for a complex movement to be correctly coded is relevant here, because it raises another important question: how does the central nervous system integrate multiple proprioceptive feedback signals to build up a single, conscious perceptual picture of the movement being performed?

In previous psycho-physiological studies (Roll and Gilhodes 1995; Roll et al. 1996), we established that, by applying complex patterns of vibration to the wrist muscles of human subjects, it was possible to induce the illusion that they were drawing geometrical figures in the complete absence of any actual hand movements. In order to elicit complex kinesthetic illusions of this kind, it was necessary to either synchronously or successively activate all the main wrist-muscle groups by applying patterns of vibration with varying frequencies. It, therefore, emerged indirectly from these behavioral studies that natural proprioceptive feedback is probably organized on the basis of the activity of the muscle-spindle populations belonging to all the muscles involved. In addition, we assumed that the peripheral coding of any motor trajectory might be based on a similar population vector code to that previously described in the case of the somatosensory neurons in the monkey cortex (Kalaska et al. 1983, 1990; Caminiti et al. 1991; Georgopoulos et al. 1993).

In order to determine how the proprioceptive sensory codes underlying the perception of complex 2-D movements are organized, we directly recorded the muscle-spindle activity originating from four of the main ankle-muscle groups during various 2-D geometrical trajectories imposed on the tip of the left foot, using the microneurographic method. In addition, the spindle activities recorded were correlated with the spatial trajectories of the extremity of the foot, rather than simply with the changes in the ankle angle, as done in most previous microneurographic studies (Roll and Vedel 1982; Hulliger et al. 1985; Burke et al. 1988; Vallbo and Al Falahe 1990).

One of the reasons why it was decided to correlate the spatial trajectory of the movements with neural activities was that cortical recordings on monkeys have shown that some movement parameters are reflected in the activity of populations of neurons and that, by using a vector model, it is possible to express neuronal activity in spatial terms (Caminiti et al. 1991; Kalaska 1991; Georgopoulos et al. 1993; Schwartz 1993). More specifically, it has been established that, during drawing movements, the cortical activity occurring during the hand-path can be accurately described by a series of population vectors calculated during the task (Schwartz 1992, 1993), i.e., by the sum vector pointing instantaneously in the direction of the actual movement, the length of which corresponds to the instantaneous speed. In the present study, using a similar vector modeling procedure, we hypothesized that the patterns of activity of the muscle-spindle populations belonging to all the muscles associated with a given joint may reflect the instantaneous direction of any motor trajectory as early as the peripheral level.

## Material and methods

Since the material and methods used in this study were very similar to those used in the companion paper (Bergenheim et al. 2000), they will be only briefly outlined in this paper (for further details, see Bergenheim et al. 2000).

Fourteen young voluntary subjects (aged 22–28 years) participated in this study, which was duly approved by the local ethical committee. The activity of a total number of 44 muscle spindle afferents (36 Ia, eight II) was recorded using the microneurographic method at the level of the Lateral peroneal nerve. These units belonged to the Tibialis anterior (T.A.; 13 Ia, three II), Extensor digitorum longus (E.D.L.; 18 Ia, four II), Extensor hallucis longus (E.H.L.; three Ia) and Peroneus lateralis (P.L.; three Ia, one II) muscles. The experimental set-up (see Fig. 1A), the recording procedure and the criteria adopted to classify the units were all the same as those described in Bergenheim et al. 2000).

The subject's left foot was attached to a rotating pedal driven by a computer-controlled machine. With this machine, it was possible to impose 2-D geometrically shaped movements, i.e., movements describing circles, squares, triangles, and horizontal and vertical ellipses. These movements were imposed at random and performed in either the clockwise or counterclockwise direction from the same starting position. The scale of all these geometrical figures was such that they fitted a 50×50-mm frame corresponding to the maximum vertical and horizontal displacements of the foot tip (Fig. 1B). They were imposed at a constant velocity of 38.5 mm/s.

### Data analysis

The analysis consisted of determining the instantaneous discharge frequency of each unit at eight evenly distributed points along the trajectory and of establishing which portion of the trajectory corresponded to the activation of each unit. In a second step, all the data collected were processed with the aim of formulating a "neuronal population vector model" (see Bergenheim et al. 2000). For this purpose, the instantaneous discharge frequencies of all the units belonging to the same muscle were averaged at each point on each trajectory. This yielded a "population vector", the orientation of which was the preferred direction of the muscle under consideration and the length of which was equal to the mean activity of all the units. This procedure was carried out for the investigated muscles (T.A., E.D.L., E.H.L., and P.L.) using the microneurographic method. In the case of the two remaining ankle muscles, which did not lend themselves to microneurography, namely the Tibialis posterior (T.P.) and Gastrocnemius soleus (G.S.) muscles, the population vectors were modeled by taking the activities of the E.D.L. and E.H.L. muscle afferents as templates (see Bergenheim et al. 2000).

Each point on any of the trajectories was, therefore, denoted by a series of six weighted population vectors, the sum of which ("sum vector") was expected to point in the direction of the tangent to the trajectory ("theoretical vectors") at this point. This assumption was tested statistically by performing a *V* test (Batschelet 1981).

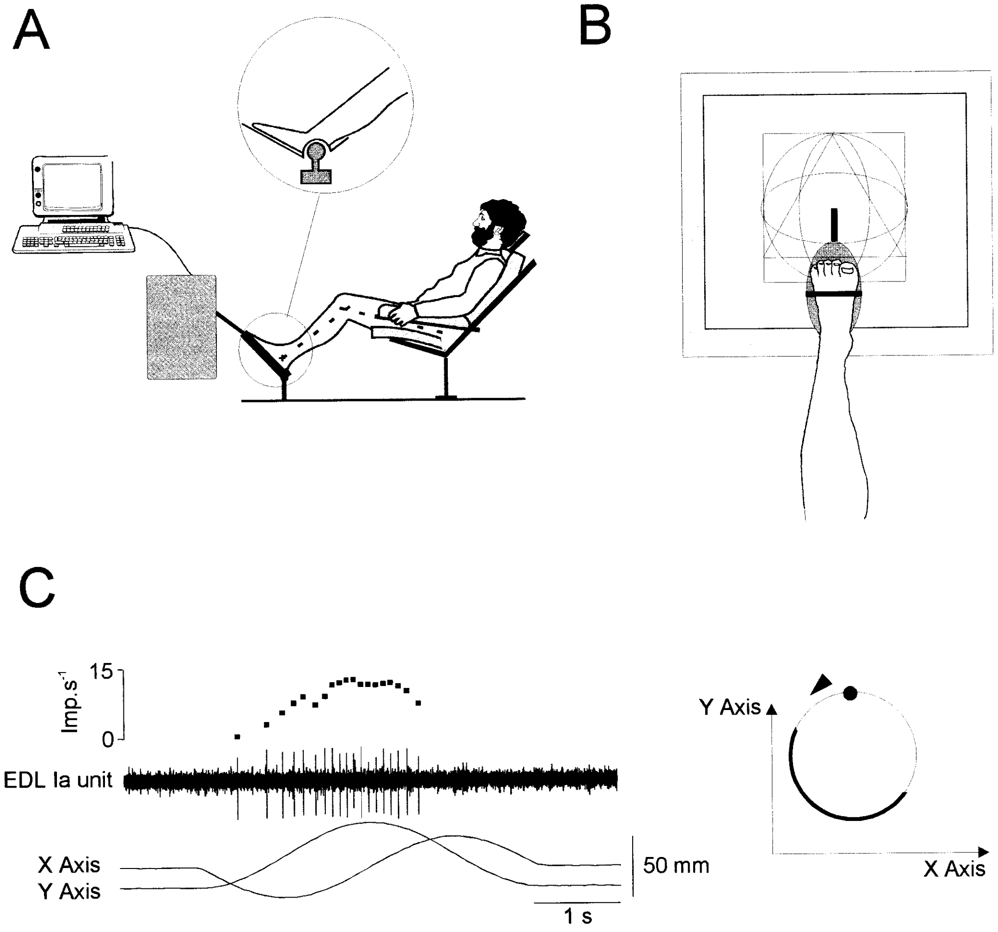


**Fig. 1A–C** Experimental setup. **A** Position of the subject and computer-controlled machine for imposing two-dimensional trajectories on the foot. **B** "Drawing-like" trajectories imposed on the tip of the subject's foot. **C** Example of a recording of a primary muscle-spindle afferent originating from the Extensor digitorum longus (*EDL*) muscle during a circular, counterclockwise trajectory (constant velocity 38.5 mm/s). The nerve signal, which was converted into an instantaneous frequency curve, was recorded together with the x and y positions of the foot extremity. The *heavy part* of the circle (shown on the *right*) corresponds to the part of the circular trajectory during which primary-afferent activity occurred

## Results

### Single unit activity during "drawing-like" movements

As an example, Fig. 2 gives the afferent activity of a primary muscle-spindle ending originating from the E.D.L. muscle during counterclockwise "drawing-like" movements and describing a straight line and various rectilinear and curvilinear figures, such as a circle, horizontal and vertical ellipses, a square, and a triangle. During all these movements, the spindle activity showed conspicuous changes only during parts of the movement trajectories. More specifically, the unit was activated only during that part of the trajectory where the direction fell into the preferred sensory sector of the receptor-bearing muscle, and its maximum discharge frequency was always reached when the movement pointed in the so-called preferred sensory direction of this particular unit (see Bergenheim et al. 2000). As can be seen in this figure, the discharge patterns were generally specific to each category of drawing movement: stretch-like patterns occurred during the drawing of both the straight line and the various rectilinear figures, and curvi-shaped patterns when curvilinear figures were being drawn. Upon analyzing the afferent discharge pattern of each individual unit, they were all found to show these general features.

The units in the three synergistic muscles located in the anterior part of the ankle (T.A., E.H.L., E.D.L.) behaved in a similar way, since their preferred sensory sectors were found to resemble each other very closely (see Bergenheim et al. 2000). Since the muscles in the posterior part of the ankle, such as the P.L. muscle, have preferred sensory sectors which lay in the opposite direction, this resulted in the units being activated during a different portion of the trajectory. This is illustrated in Fig. 3, which gives the responses of four primary endings originating from the E.D.L., E.H.L., T.A., and P.L. muscles during the same triangular (Fig. 3A) and elliptical (Fig. 3B) movement trajectories. As can be seen, the primary afferent activities in the three anterior muscles increased during the drawing of the two first sides of the triangle, and then stopped, and were relayed by the P.L. primary afferent. Generally speaking, none of the individual primary endings ever fired throughout the entire geometrical trajectory: the coding of the whole path always involved partly redundant and successive primary-afferent activities corresponding to the various muscles surrounding the ankle joint. On the other hand, all the secondary endings tested behaved differently, since they were generally able to encode the entire trajectory simply by modulating their discharge frequency so that the maximum frequency occurred in the preferred senso-

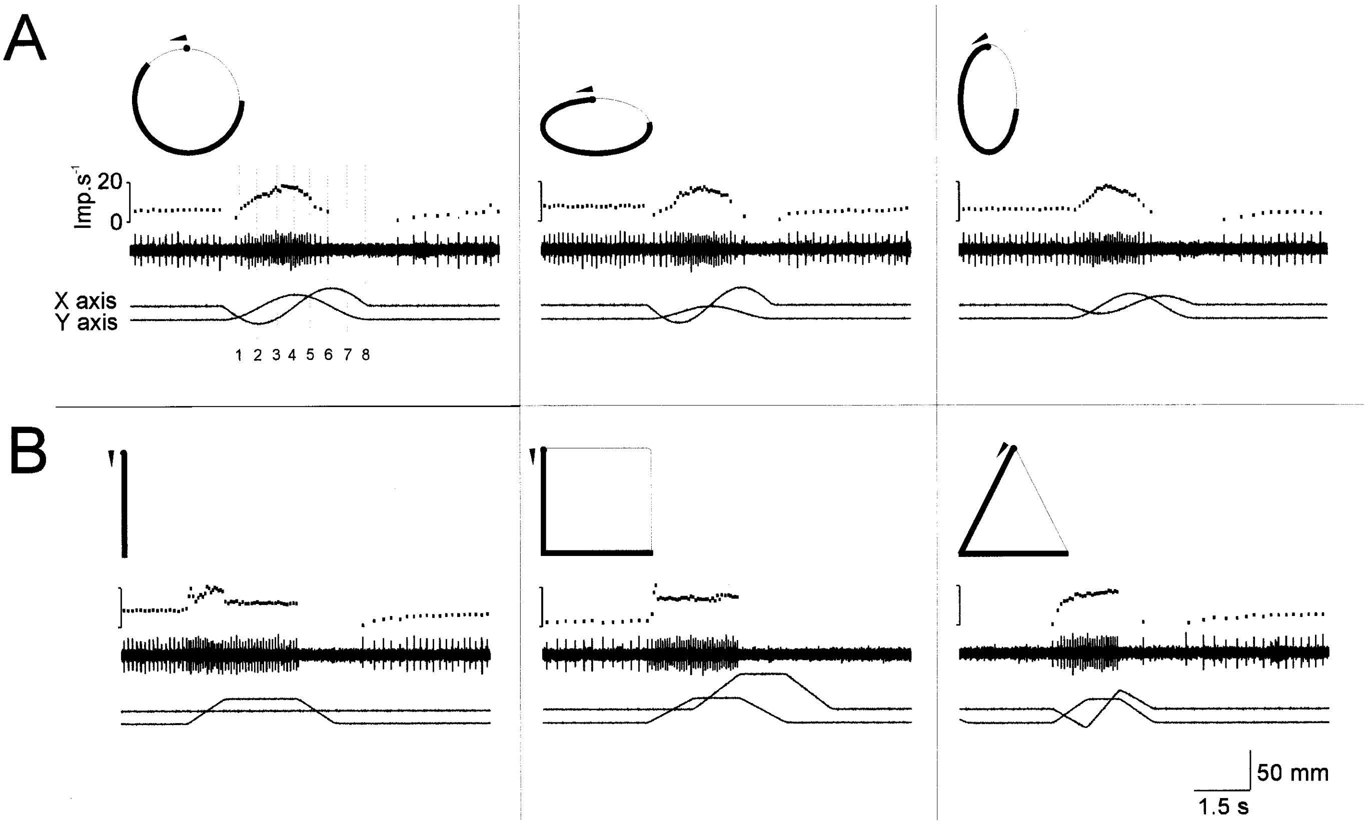


**Fig. 2** Examples of recordings of the activity of a single Extensor digitorum longus (E.D.L.) primary muscle-spindle afferent during various curvilinear (**A**) and rectilinear (**B**) geometrical trajectories imposed on the tip of the foot in the counterclockwise direction. The *heavy lines* on the trajectories indicate the part during which the primary afferent was activated. Note the curvi-shaped instantaneous frequency curves recorded during the drawing of curvilinear shapes and the stretch-shaped ones recorded during the rectilinear trajectories

ry sector of each receptor-bearing muscle. These general features were found to be very similar with all the geometrical shapes drawn here, as shown in the case of the elliptical shape in Fig. 3B.

Table 1 gives the percentage of the entire path perimeter corresponding to spindle activity in the case of the primary and secondary endings belonging to each muscle with each category of figure (curvilinear and rectilinear) and in both movement directions (clockwise and counterclockwise). It emerged from the analysis that there existed a significant difference between the primary and secondary afferents, the activity of which covered, on average, 49.2% and 84.8% of the entire trajectory, respectively. These percentages did not vary significantly whether curvilinear or rectilinear figures were being drawn or whether the drawing was performed in the clockwise or counterclockwise direction.

## Population coding of curvilinear and rectilinear trajectories

With all the primary and secondary endings tested, the geometrical trajectories were all systematically imposed on the ankle joint as long as the recording remained stable. In order to investigate the muscle-spindle coding of a movement trajectory, the data on each receptor-bearing muscle were first pooled, so as to quantify the contribution of that muscle, and the contribution of all the muscles acting together on the ankle joint was evaluated in a second step.

The activity of each afferent was, therefore, first determined by calculating its instantaneous discharge frequency at eight evenly distributed points on each movement trajectory (see Fig. 2A). Secondly, the values obtained on all the units belonging to the same muscle were averaged. Each geometrical shape could, therefore, be described by a series of mean firing rates based on all the units corresponding to one muscle. This is illustrated in Fig. 4 in the case of a circular movement imposed in the counterclockwise direction. The coding of the movement trajectory in terms of the mean instantaneous discharge frequency is given here by thin lines. The preferred sensory sectors are indicated on the diagrams by heavy lines, each of which corresponds to one of the muscles tested (see Bergenheim et al. 2000), and the preferred sensory direction by dotted lines. With all the muscles tested, the preferred sensory sectors and the curve describing the mean frequency changes during the trajectory at the eight pre-selected points were almost

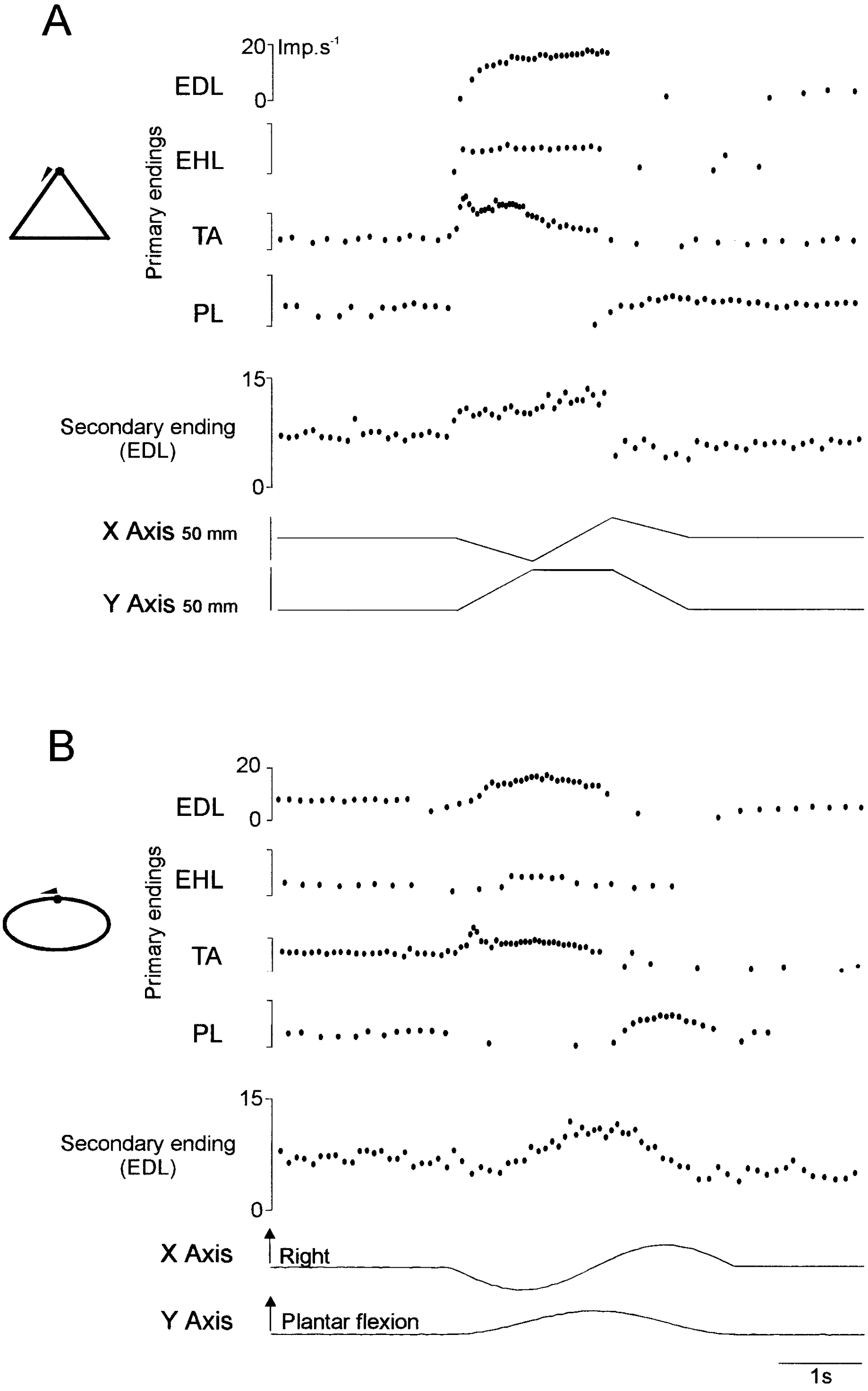
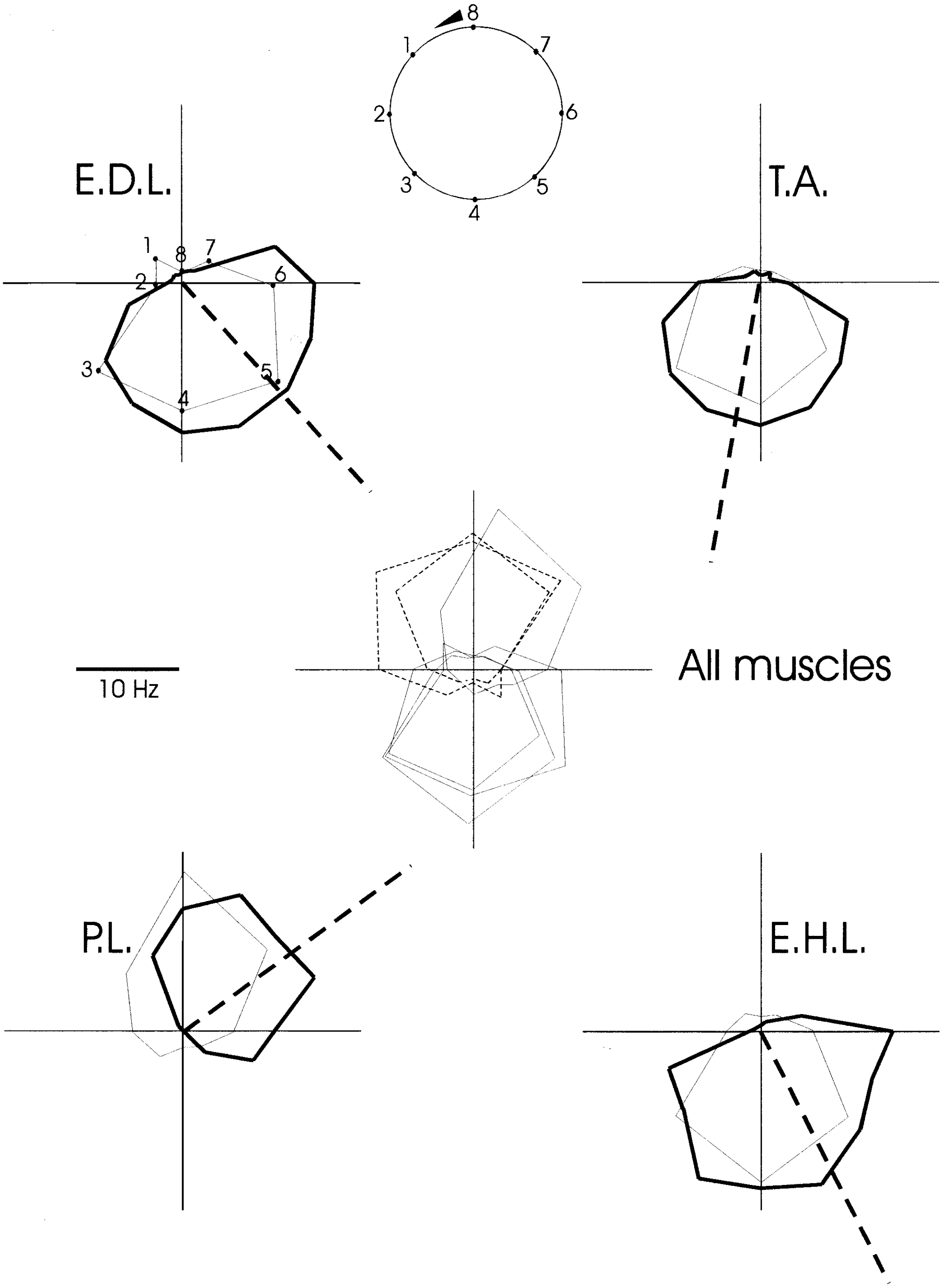


**Fig. 3** Examples of recordings of the activity of four muscle-spindle primary endings originating from the Extensor digitorum longus (*EDL*), Extensor hallucis longus (*EHL*), Tibialis anterior (*TA*), and Peroneus lateralis (*PL*) muscles and a muscle-spindle secondary ending from the Extensor digitorum muscle during a triangular counterclockwise trajectory (**A**) and a horizontal counterclockwise elliptical trajectory (**B**) imposed on the tip of the foot. Note that, during both trajectories, the primary endings originating from the three muscles in the anterior part of the leg showed redundant behavior, since their discharge rates increased during the first two thirds of the trajectory. The primary ending from the Peroneus lateralis took over the task of coding the last third of the trajectory. The discharge frequency of the secondary ending was only slightly modulated during most part of both trajectories

**Table 1** Percentages of the entire path perimeter corresponding to spindle activity in the case of the primary (Ia) and secondary (II) endings belonging to each muscle with each category of figure (curvilinear and rectilinear) in both directions (clockwise and counterclockwise). *TA* Tiblialis anterior, *EDL* Extensor digitoum longus, *PL* Peroneus lateralis, *EHL* Extensor hallucis longus

| | All shapes | | Curvilinear (Ia) | | Rectilinear (Ia) | |
|---|---|---|---|---|---|---|
| | Ia | II | Clockwise | Counterclockwise | Clockwise | Counterclockwise |
| TA | 45.1 | 100.0 | 42.9 | 44.2 | 48.3 | 46.7 |
| EDL | 54.0 | 84.4 | 47.7 | 58.9 | 50.4 | 56.7 |
| PL | 26.8 | 56.0 | 26.7 | 53.7 | 28.4 | 36.1 |
| EHL | 64.8 | | 71.0 | 58.7 | 76.0 | 63.0 |
| All muscles | 49.2 | 84.8 | 45.6 | 50.0 | 49.3 | 51.6 |

**Fig. 4** Mean frequency curves of Ia afferents originating from the Extensor digitoum longus (*E.D.L.*), Peroneus lateralis (*P.L.*), Extensor hallucis longus (*E.H.L.*), and Tiblialis anterior (*T.A.*) muscles during a counterclockwise circular trajectory imposed on the tip of the foot (constant speed 38.5 mm/s). The mean instantaneous frequencies for all the units belonging to the same muscle were calculated at eight points on the trajectory (*1–8*). It is represented by *thin lines*. The *heavy curves* give the preferred sensory sectors of the various muscles and the *dashed line* the corresponding preferred sensory directions, as defined in Bergenheim et al. (2000). Note the almost good angular superimposition obtained between the mean frequency curves and the preferred sensory sector with each of the ankle muscles. On the central graph, the mean frequency curves of all the ankle muscles were combined. The *dashed curves* corresponded to the activity of the Tibialis posterior and Gastrocnemius soleus muscle spindles, which was modeled as described in Bergenheim et al. (2000)



completely superimposed. In other words, a given primary muscle-spindle population was activated during any trajectory only in that muscle's preferred sensory sector, i.e., when the instantaneous direction of the trajectory, which can be described by the tangent to the curve, fell within the preferred sensory sector. In addition, when all the mean curves obtained with all the ankle muscles were combined on the same graph (center graph in Fig. 4), it can be seen that most part of the 360° trajectory was encoded and that the various sensory sectors sometimes overlapped considerably, especially in the case of adjacent muscles.

### The "vector model" as a means of describing the proprioceptive population coding of geometrical trajectories

The results were further analyzed using the "vector model" previously used to describe population coding at the cortical level (Georgopoulos et al. 1984; Kalaska et al. 1990) and the perceptual integration of proprioceptive information (Roll and Gilhodes 1995; Roll et al. 1996). This involved denoting by vectors the contribution of muscle-spindle populations in each ankle muscle to the coding of a given trajectory.

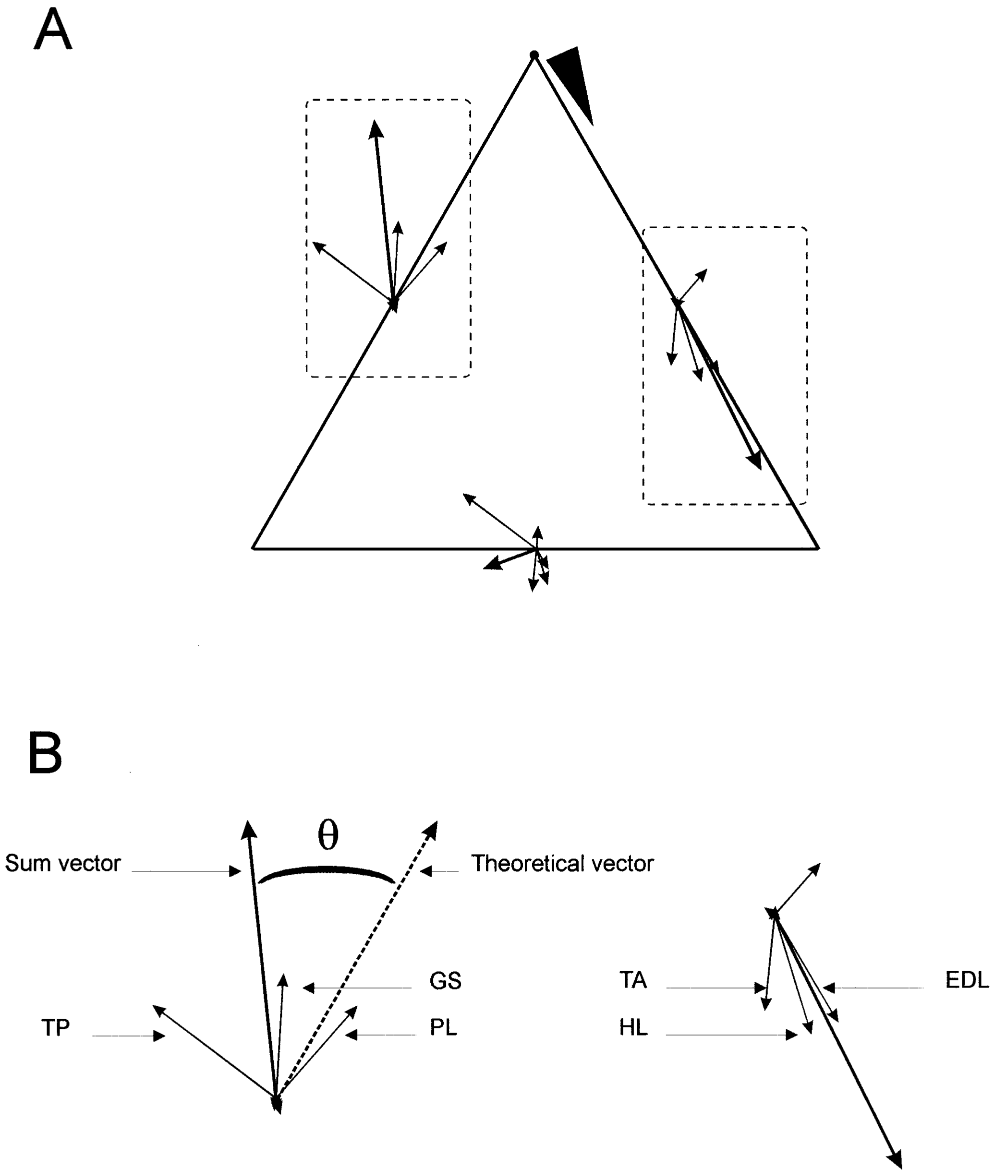


**Fig. 5** **A** Vector diagram of muscle-spindle populations during a clockwise triangular trajectory (constant speed 38.5 mm/s). Each population vector (*thin vector*) is oriented in the preferred sensory direction of the corresponding receptor-bearing muscle and has a module corresponding to the mean instantaneous frequency recorded at three characteristic points on the trajectory. The *heavy vectors* are the sum vectors calculated at each point on the trajectory. Note that their orientation varied, depending on the direction of the path. **B** Detailed diagram of population vectors, sum vector, and theoretical vector corresponding to two particular points on the trajectory (*dashed squares* in **A**). The theoretical vector is the tangent to the trajectory at this point, and θ is the angular difference between the experimental sum vector and the theoretical vector. *TP* Tibialis posterior, *GS* Gastrocnemius soleus, *PL* Peroneus lateralis, *EDL* Extensor digitoum longus, *HL* Extensor hallucis longus, *TA* Tiblialis anterior

At a given point on the movement trajectory, a population vector was calculated: its direction was taken to be the preferred sensory direction of the receptor-bearing muscle and its length, the mean instantaneous frequency of that population of units. Six population vectors were calculated in the same way, corresponding to the instantaneous oriented and weighted contribution made by each muscle to the coding of the trajectory. Four of the six vectors (E.H.L., E.D.L., T.A., P.L.) were directly calculated on the basis of microneurographic recordings as mentioned above, and, in the case of the remaining muscles acting on the ankle joint (G.S. and T.P.), the vectors were deduced by modeling their preferred sensory direction and their mean frequency, based on the effects of the vibration-induced illusions and the data from the template muscles (see Bergenheim et al. 2000).

Figure 5 gives, as an example, the individual population vectors of each muscle (thin lines) at three characteristic points on the triangular trajectory imposed in the clockwise direction. Here, the weight of one particular population vector can be clearly seen to have depended on the orientation of the movement. At each point on each movement trajectory, the six population vectors were summed together and the orientations of the sum vectors (heavy lines) were compared with those of the tangents to the trajectory at the same points (called the “theoretical vector” in Fig. 5B). As can be seen, the orientations of the sum vectors were related to the trajectory orientations (mean difference among all the shapes: 42.4°).

The sum vectors are furthermore illustrated in Fig. 6 in the case of elliptical shapes performed in the clockwise (right) and counterclockwise (left) directions. Generally speaking, it could be seen that, even when the direction of the sum vectors differed from that of the theoretical vectors, their orientation resembled that of the trajectory. In fact, the crossing of the same point on the trajectory in either the clockwise or counterclockwise

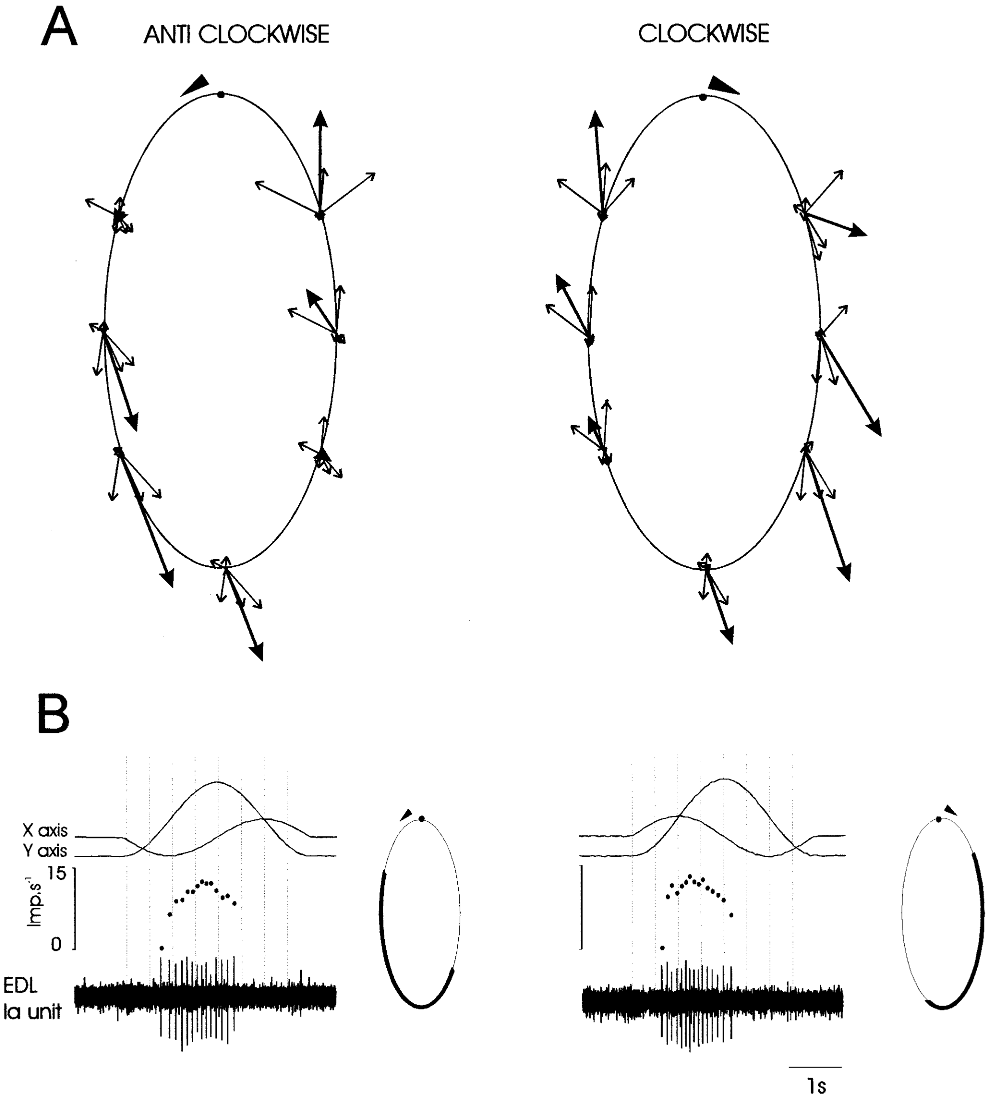


**Fig. 6A, B** Changes in the population and sum vectors during the performance of elliptical counterclockwise (*left*) and clockwise (*right*) trajectories. The corresponding *lower graphs* give, as an example, the activity of a primary afferent originating from the Extensor digitorum longus muscle (*EDL*) during the latter trajectories. The *heavy part* of each trajectory is the part during which the primary afferent was activated. Note the permanent re-orientation of the sum vectors and their opposite directions during clockwise and counterclockwise trajectories

direction led to a re-orientation of the sum vector of 115°, on average, instead of the 180° expected theoretically.

A circular statistical analysis ($V$ test) was conducted on all the data in order to determine how accurately the direction of the movements was coded on the basis of all the proprioceptive feedback information arising from all the muscles acting on a joint. The results of this test were highly significant ($u$=6.44, $n$=65, $P$<0.0001), which indicated that the sum vectors pointed around the expected directions.

In conclusion, the proprioceptive coding of these geometrical trajectories seems to have been based on a multi-population coding process, whereby each individual muscle-spindle population provided weighted, oriented information contributing to defining the parameters of the ongoing trajectory.

## Discussion

In a recent paper, Verschuren et al. (1998) claimed that, in humans, “It has so far been impossible to record from ensembles of muscle spindle afferents and that, consequently, the representation of movement parameters by ensemble of receptors has been limited to studies of perception”. The results presented in this paper probably constitute a first step towards overcoming this difficulty by recording from muscle-spindle afferents originating from different muscles in humans and by showing that the central nervous system is fed with successively relayed primary-afferent feedback inputs arising from all the different muscles working on a given joint. This approach was first suggested by results based on vibration-induced illusions of spatially oriented movements and the drawing of geometrical figures evoked at the hand level in human subjects (Roll and Gilhodes 1995; Roll et al. 1996). It was also suggested by these studies that it might be possible to denote the direction and velocity of the perceived movements by the population vector of the vibration-induced muscle-spindle inputs arising from the entire set of muscles acting on a given joint. Upon addressing the same general question, i.e., “what role is played by the ensemble of muscle spindles within the same muscle or within synergistic muscles?”, Verschuren et al. (1998), by selectively perturbing calibrated hand movements via vibration, recently showed that the performance errors were larger when combinations rather than individual muscle tendons were vibrated. Given that the performance of a motor task requires perception of both the joint velocity and position of the wrist, these authors suggested that kinesthesia may be derived from the integrated inputs from muscle spindles located in all the synergistic muscles crossing a joint, in line with previous findings on perception (Roll and Gilhodes 1995).

## The primary spindle afferent feedback from one muscle does not suffice to completely specify the entire trajectory

All the previous studies dealing with the proprioceptive coding of movement have focused on a single spatial direction (i.e., on the stretching or shortening of a receptor-bearing muscle under either passive or active conditions) (Hagbarth and Vallbo 1968; Roll and Vedel 1982; Hulliger et al. 1985; Burke et al. 1988; Ribot-Ciscar and Roll 1998). By using a computer-controlled machine to impose a variety of 2-D movements on a specific joint, we were able here to make a qualitative jump, yielding new insights into the organization of proprioceptive feedback during complex motor trajectories, such as those involved in drawing 2D geometrical shapes.

One of the most striking points emerging from the present study is that each individual primary afferent started to fire as soon as the instantaneous direction of the ongoing trajectory entered the preferred sensory sector of the receptor-bearing muscle and stopped firing when the ongoing movement left this sector. Consequently, the notion of a preferred sensory sector determined on the basis of linear and differently oriented movements (see Bergenheim et al. 2000) can be extended to all kinds of motor shapes described by a joint during the performance of a drawing task. As can be seen in Fig. 4, the distribution of the preferred sensory sectors was not perfect. This might be explained by the fact that we focused in this study only on the main muscles acting on the ankle joint. It seems likely that a more uniform distribution would be obtained if all the muscles (including the smaller muscles, e.g., the Extensor digitorum brevis, Fibularis brevis, and Fibularis longus) were taken into account. The question as to how the entire trajectory of a given geometrical figure is encoded in sensory terms can, therefore, probably be answered by the fact that the CNS receives the successive primary spindle inputs from the various muscles groups surrounding the joint as they are stretched one after the other during the trajectory.

These results shed light on previous data on the illusions of drawing evoked at hand level by applying specific patterns of vibration to the four main wrist muscle groups (Roll and Gilhodes 1995; Roll et al. 1996). In view of the neurosensory data presented in the present paper, it is now easier to understand why, for example, to be able to induce an illusion of curvilinear figure drawing, it was necessary to co-vibrate two adjacent muscle groups and to increase the vibration frequency applied to the one muscle while applying a decreasing frequency to the other. When this pattern of vibration is applied to all the successive pairs of adjacent wrist group muscles, the sensation elicited is, therefore, one of “circle-like” drawing.

Contrary to the primary endings, the secondary ones were found to be active during almost the entire “drawing-like” path and modulated their activity inside the preferred sensory sector of their receptor-bearing muscle. This specificity of the secondary endings is probably due to their high degree of position sensitivity and to the fact that they generally do not fall silent during muscle shortening (Vallbo 1973; Burke et al. 1988). Consequently, it seems likely that the secondary afferent feedback may convey information about the location of the ongoing trajectory within the subject’s working space. Unfortunately, since only a few secondaries were recorded, this issue remains to be investigated.

In short, the on-line coding of complex geometrical trajectories can be said to constitute a collective task, during which each of the primary spindle populations from each muscle is mobilized in turn. From this point of view, the sensory coding of a movement on the basis of proprioceptive feedback might directly reflect the anatomical organization of the joint involved. The anatomical structure of a joint determines the spatio-temporal pattern of muscle stretching and shortening, which in turn gives rise to a multipopulation proprioceptive pattern. The coding of a trajectory in either the clockwise or counterclockwise directions might, therefore, differ, depending on the order in which the muscles involved are stretched.

## The afferent inputs from all the muscles acting on a joint encode the instantaneous direction of any trajectory

As early as 1984, Georgopoulos and his collaborators proposed a “vector model” for describing the relationship between the activity of motor cortical-cell populations and some specific movement parameters. Since then, this model has been amply used to study the activity of population of neurons on both the motor areas (Kalaska 1991; Schwartz 1992, 1994) and the sensory areas (Kalaska 1991; Ruiz et al. 1995) on the cortical level. In this context, studies should be also mentioned which showed that motor cortical cells do not exclusively signal information in extrinsic space, but also in intrinsic one (Mussa-Ivaldi 1988; Scott and Kalaska 1997).

In the present study, we used the vector model to determine whether the parameters of a given drawing trajectory are already encoded at the peripheral level by populations of muscle spindles originating from the set of muscles with which a joint is equipped, i.e., very intrinsic information, which would also support an extrinsic coordinate coding.

In a recent study by Schwartz (1992), it was reported that the mean activity of individual neurons in the motor cortex varied with the instantaneous direction of an ongoing drawing task and that there exists a cosine-tuning function between the movement direction and the discharge frequency. Moreover, it was shown that the directions of both movement and population vectors changed continuously during the drawing of spirals (Schwartz 1994). Area-5 proximal-arm cells showed the same variations in their activity with the hand path as did the motor cells, the only difference being that most of them discharged only after the onset of movement and appeared to be strictly "sensory" (Seal et al. 1983; Kalaska 1991). These properties suggest that a representation of natural movement trajectories might be built up in this area on the basis of multiple proprioceptive inputs generated by the movement itself (Mountcastle et al. 1975; Kalaska et al. 1983; Burbaud et al. 1991; Battiglia-Mayer et al. 1998). Here, we established that, as early as the muscle-afferent level, the mean activity of a muscle-spindle population also varies with the instantaneous orientation of the drawing trajectory and that this variation in the muscle-spindle activity also obeys a cosine-shaped function. Moreover, at each point on the ongoing geometrical-shaped trajectory, the sum vector expressing the contribution of all the units belonging to all the ankle muscles was found to have a similar orientation to that of the tangent to the trajectory. Certainly, the matching of the calculated population vectors and the theoretical vectors was not perfect (in particular those seen for the inversion/eversions in Fig. 6). There may have been several reasons for this imperfect matching. First, the muscle-spindle activity was not exactly cosine tuned, and the preferred directions were not exactly uniform (Sanger 1994). When the afferent data were analyzed by means of a multiple linear-regression method, the accuracy of the instantaneous direction determination was about 15% greater. Secondly, the number of units tested here was relatively small (44 units) in comparison with the numbers generally tested at cortical level (300–400 units in Schwartz's 1993 study), and the units differed quantitatively from one muscle to the other. Third, the preferred sensory direction was determined with a fairly broad angular step of 15°. Four, the movements were passively imposed on the ankle, thus reducing the amount of gamma drive (Hulliger 1984; Ribot-Ciscar and Roll 1998).

To summarize, as concerns the proprioceptive coding of geometrically shaped movement trajectories, the primary afferent feedback information arising from a single muscle does not suffice to completely encode the entire trajectory, since the muscle receptors in a given muscle respond only when the tangent to the ongoing movement falls within that muscle's preferred sensory sector. However, during any movement trajectory, each muscle makes an instantaneous, oriented, and weighted contribution to the sensory coding of the movement direction. The population coding process involved can be described by the instantaneous sum vector, the orientation of which is constantly updated, depending on the direction of the ongoing movement.

Lastly, the results of these two companion papers, the one dealing with spatially oriented and the other with "drawing-like" movements, strongly suggest that kinesthesia is based on the simultaneous processing of the information from populations of muscle spindles originating in all the muscles surrounding a joint. The question as to whether such a multi-muscle proprioceptive processing is applicable during 2-D active movements will be addressed in further studies.

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