Inducing Any Virtual Two-Dimensional Movement in Humans by Applying Muscle Tendon Vibration

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Roll J-P, Albert F, Thyrión C, Ribot-Ciscar E, Bergenheim M, Mattei B. Inducing any virtual two-dimensional movement in humans by applying muscle tendon vibration. J Neurophysiol 101: 816–823, 2009. First published December 3, 2008; doi:10.1152/jn.91075.2008. In humans, tendon vibration evokes illusory sensation of movement. We developed a model mimicking the muscle afferent patterns corresponding to any two-dimensional movement and checked its validity by inducing writing illusory movements through specific sets of muscle vibrators. Three kinds of illusory movements were compared. The first was induced by vibration patterns copying the responses of muscle spindle afferents previously recorded by microneurography during imposed ankle movements. The two others were generated by the model. Sixteen different vibratory patterns were applied to 20 motionless volunteers in the absence of vision. After each vibration sequence, the participants were asked to name the corresponding graphic symbol and then to reproduce the illusory movement perceived. Results showed that the afferent patterns generated by the model were very similar to those recorded microneurographically during actual ankle movements (r = 0.82). The model was also very efficient for generating afferent response patterns at the wrist level, if the preferred sensory directions of the wrist muscle groups were first specified. Using recorded and modeled proprioceptive patterns to pilot sets of vibrators placed at the ankle or wrist levels evoked similar illusory movements, which were correctly identified by the participants in three quarters of the trials. Our proprioceptive model, based on neurosensory data recorded in behaving humans, should then be a useful tool in fields of research such as sensorimotor learning, rehabilitation, and virtual reality.

INTRODUCTION

Muscle proprioception along with vision and touch contribute to position sense and kinesthesia. Concerning proprioception, the muscle spindles feed the CNS with signals about changes in the length of bearing muscles for both sensorimotor and perceptual purposes (Cordo 1990; Edin and Johansson 1995; Gandevia 1996; Gandevia and Burke 1992; Jones et al. 2001; Radovanovic et al. 2002; Roll et al. 2000). However, it remains unknown how the CNS collects the proprioceptive feedback arising from all the muscles surrounding a particular joint and how it integrates this information to build up a picture of the movement being performed.

Neurosensory and psychophysical data have shed light on these complex proprioceptive sensory codes and the associated perceptual events. First, microneurography serves to record feedback messages triggered in populations of afferents from all the muscles surrounding a given joint in response to two-dimensional movements performed under active and passive conditions (Bergenheim et al. 2000; Cordo et al. 2002; Jones et al. 2001; Roll et al. 2000, 2004). In addition, the “population vector model,” first used at the cortical level (Georgopoulos 1982), was adapted to ensembles of somesthetic sensory neurons and to the particular anatomical and physiological organization of the cutaneous and muscular systems (Aimonetti et al. 2007; Bergenheim et al. 2000; Jones et al. 2001; Roll et al. 2000). Indeed, the muscle spindle population merges into a very homogeneous population inside the muscle that bears them. These studies showed that each muscle spindle responds only to a specific range of movement directions (the Preferred Sensory Sector) and exhibits maximum sensitivity in a specific direction (the Preferred Sensory Direction). When moving away from this direction, the receptor’s activity is decreasingly cosine tuned. The mean activity of a muscle spindle population throughout a movement trajectory is represented by a “population vector.” The direction of this population vector is the Preferred Sensory Direction of a given muscle (i.e., the average of the preferred sensory directions of all the muscle spindles in that muscle), whereas its module is proportional to the mean firing rate. By taking the sensory activity originating from all the muscles of a given joint, it was demonstrated that the neurosensory sum vectors are highly correlated with the movement vectors at any point of a given trajectory (Albert et al. 2005, 2006; Bergenheim et al. 2000; Jones et al. 2001). Consequently, each sum vector gives the instantaneous direction and velocity of the ongoing movement (i.e., its tangential velocity).

Moreover, muscle vibration activates the Ia muscle spindle in a one-to-one ratio and induces illusions of movements in the 1- to 100-Hz frequency range (Burke et al. 1976; Goodwin et al. 1972; Roll and Vedel 1982; Roll et al. 1989). Such a link between sensory and kinesthetic events has been particularly attested by Ia afferent feedback recordings during an ankle movement, which evoked the illusion of the same movement when reapplied to the participant via muscle vibration (Albert et al. 2006).

This corpus of data obtained at both neurosensory and perceptual levels (Albert et al. 2006; Bergenheim et al. 2000; Roll et al. 2000, 2004) led us to develop a model mimicking proprioceptive inputs that can be used to induce any virtual two-dimensional movement. Since the movement vectors describing the movement trajectories are highly correlated with the neurosensory sum vecc...
tors (Albert et al. 2005, 2006; Bergenheim et al. 2000), we decided here to use a procedure backward: each sum vector is decomposed into a series of population vectors giving the mean discharge frequency of the afferents in each muscle at any moment. These population vectors represent the oriented and weighted contribution of each receptor population to the instantaneous coding of the ongoing movement.

We first compared the mean natural afferent patterns recorded microneurographically and the patterns generated by the model. Second, we compared the illusory trajectories evoked using our proprioceptive model with those induced at ankle level by piloting the vibrators by means of prerecorded Ia afferent patterns (Albert et al. 2006). Last, we investigated the effectiveness of this model for another joint, the wrist.

M E T H O D S

General experimental setup

Three sets of vibration patterns were used to activate the tendon of the main ankle and wrist muscle groups to induce the corresponding illusory movement (see Fig. 1). The first one, experiment 1, reported from Albert et al. (2006), presents the set of vibrations directly based on the muscle spindle afferent responses previously recorded using the microneurographic method. On the other hand, experiments 2 and 3 are specific to the present study and present the sets of vibrations generated by the proprioceptive model at the ankle and wrist levels.

After experiencing the illusions, the participants were asked to name the shape of the trajectory they had perceived before drawing it on a digitizing tablet.

Experiment 1 was carried out on 10 healthy volunteers. Experiments 2 and 3 were each carried out on 10 healthy human volunteers (5 males, 5 females). These participants were selected because they previously experienced kinesthetic illusions during muscle tendon vibration. All the participants gave their informed consent to the procedure as required by the Helsinki declaration. This study was approved by the local ethics committee (CCPPRB, Marseille I).

The participants were comfortably seated in an armchair, holding a pencil in their right hand. The tip of the pencil was in contact with a digitizing tablet. The participants had their legs in a standardized relaxed position with both feet resting on stationary pedals. The left ankle was kept at an angle of 90°. In experiments 1 and 2, five electromagnetic vibrators (Vibralgic model, Electronic Conseil, Alès, France) were fixed to adjustable devices so that the vibrators could be positioned perpendicularly to the tendons of the left ankle joint muscles with a pressure of about 0.5 N. In experiment 3, four vibrators were fixed with the same pressure perpendicularly to the tendons of the muscle groups of the right wrist joint. The heads of the vibrators were 1 or 2 cm long, depending on the size of the tendon vibrated, and were 0.6 cm in diameter. The vibration was delivered via two multichannel electronic devices connected to high-power amplifiers (pulse duration: 5 ms; amplitude: 0.25 mm peak to peak; Rematic, St-Etienne, France). The vibration frequency (1–100 Hz) was controlled by a software program (LabVIEW 6i).

Computing the vibration patterns

EXPERIMENT 1 USING MICRONEUROGRAPHIC RECORDINGS. The experimental procedures used to perform microneurographic recordings and to determine vibration patterns mimicking Ia afferent activities have been extensively described elsewhere (Albert et al. 2006; Roll...
et al. 2004). In brief, for the microneurographic experiments, participants were seated in an armchair with their right foot placed on a stationary pedal and their left foot attached to a movable pedal connected to a computer-controlled machine. This machine imposed two-dimensional movements on the ankle joint, making the tip of the foot trace various graphic symbols mimicking the kinematic parameters of movements performed by the experimenter on a digitizing tablet (see e.g. Roll et al. 2004).

During these imposed movements, the unitary activity of 55 muscle spindle afferents was recorded microneurographically at the popliteal fossa (for further details, see e.g. Bergenheim et al. 1999). Twelve of these 55 afferents were located in the tibialis anterior (TA), 17 in the extensor digitorum longus (EDL), 8 in the extensor hallucis longus (EHL), 8 in the peroneus lateralis (PL), 8 in the gastrocnemius soleus (GS), and 2 in the tibialis posterior (TP). From the data thus recorded, the mean firing pattern of the muscle spindle population in each muscle was determined during each movement. The proprioceptive input originating from each muscle was normalized with respect to the maximum firing rate in all the muscles tested (between 0 and 100 Hz). In addition, since the TA and the EHL tendons are anatomically too near each other to be vibrated separately and since their afferent patterns were found to be very similar, the responses from these muscles were averaged. The spatiotemporal patterns obtained during the above-cited recording sessions were then used to pilot each of the five vibrators applied to the TA + EHL, EDL, PL, GS, and TP muscle tendons.

EXPERIMENTS 2 AND 3 USING THE PROPRIOCEPTIVE MODEL. To compute the multipopulation patterns evoked by a specific movement (previously written by the experimenter on a digitizing tablet as in experiment 1), a set of mathematical transforms was applied to the two-dimensional trajectory of each movement. These transforms were drawn from the “population vector model” (Bergenheim et al. 2000; Georgopoulos et al. 1982, 1988; Roll et al. 2000; Schwartz 1992, 1993). First, to smooth out the signal, we applied a low-pass filter (a Hanning filter with a half-window of 0.05 s) to the limb trajectory recorded. Second, the instantaneous tangential vector components of the trajectory were determined every 200 ms using the formula $\dot{x}(t) = (x(t + 1) - x(t - 1))/2$, and likewise for $\dot{y}$. This time window was identical to the one used by Roll et al. (2004) to compute the afferent inputs recorded in microneurography. At each time point, the instantaneous velocity vector was orthogonally projected onto the previously determined Preferred Sensory Direction of each muscle using the formula: $\frac{Proj}{PSD} = \frac{ Vect }{ PSD } \cdot \cos \theta$. “Vect” is the tangential velocity vector, “PSD” is the Preferred Sensory Direction of an afferent nerve, and $\theta$ is the angle between these two vectors. “Proj” is the population vector representing the muscle spindle feedback from the muscle under consideration. This projection allowed us to simulate the cosine variations in the activity of the proprioceptive receptors of each muscle. Based on microneurographic data, the Preferred Sensory Sector of each muscle was chosen to be symmetric around the muscle’s Preferred Sensory Direction and to cover 180°. Figure 2 illustrates the modeling procedure used.

The final step of modeling was to normalize the proprioceptive input originating from each muscle in the same way as for the microneurographic recordings, that is, with respect to the maximum firing rate obtained in all the muscles tested. (This approach is under Patent number 0.8/02242.)

Thus to generate vibratory patterns that effectively induce illusory movements, all one needs to include in the model is the preferred sensory directions of the main muscle groups. Since Bergenheim et al. (2000) showed that the direction of vibration-induced illusions did not differ significantly from the Preferred Sensory Direction of the vibrated muscle, determined microneurographically, we used the preferred sensory directions previously determined for the ankle in Bergenheim et al. (2000) and for the wrist in Roll and Gilhodes (1995). In these studies, after a vibration of 80–100 Hz during 10 s for each muscle group, the participants 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. Since the variability reported in these studies is low, we decided not to take it into account in our modeling procedure. These directions for the ankle muscles: tibialis anterior [TA] + extensor hallucis longus [EHL] in blue; extensor digitorum longus [EDL] in green; peroneus lateralis [PL] in orange; gastrocnemius soleus [GS] in purple; tibialis posterior [TP] muscles in red. The gray semicircle represents the 180° around the tangential velocity vector in which the model computed sensory activities. Note that if the preferred sensory direction of one particular muscle is not within an angle of 180° around the instantaneous movement direction, the amplitude of this particular vector will be null.

Muscle tendon vibration

The optimum position of each vibrator head was carefully determined by asking the participants to keep their eyes closed and to give the direction of the perceived illusory movement during 10 s of 80-Hz muscle tendon vibration. We checked whether this direction matched the known preferred sensory direction. The participants were asked to relax, keep their eyes closed, and to focus on the illusory movement trajectory that the tip of the left foot (experiments 1 and 2) or the right hand (experiment 3) was experiencing. Prior to the vibration, they were informed about the category of movement that could be recognized, i.e., letters, numbers, or geometrical shapes. Experimental vibratory patterns (experiment 1) or modeled ones (experiment 2) inducing illusory movements forming four letters (a, b, e, n) and four numbers (1, 2, 3, 8) were applied randomly to the corresponding ankle muscle tendons of each participant. In experiment 3, modeled vibratory patterns evoking six letters (a, b, e, n, u, v), six numbers (1, 2, 3, 6, 8, 9), and four geometric shapes (circle, rectangle, square, triangle) were applied randomly to
the corresponding wrist muscle tendons of each participant. Each vibration sequence was repeated three times. After the three vibratory sequences, the participants were asked to name the movement they had just perceived and, immediately afterward, to copy this movement by drawing it by hand on a digitizing tablet. They were requested to pay special attention to the shape, velocity, and size of the illusory trajectory perceived. The movement trajectory drawn by each participant was then sampled at 200 Hz and stored for further analysis.

Data analysis

Four types of trajectories (“Initial Trajectories”; “Experimental Trajectories”; “Model Ankle Trajectories”; “Model Wrist Trajectories”) were analyzed in this study. The “Initial Trajectories” are the movement trajectories imposed during microneurographic recordings and used to compute the patterns. In experiment 1, the “Experimental Trajectories” were the participants’ drawings of the illusory movements they perceived in response to the vibration patterns generated by the proprioceptive model. Finally, in experiment 3, the “Model Wrist Trajectories” were the subjects’ drawings of the illusory movements they perceived in response to application to the wrist of the vibration patterns given by the proprioceptive model.

To validate our modeling procedure we compared, for the ankle joint, the vectors describing the Initial Trajectories with those built up from the muscle spindle feedback generated by the model. The effectiveness of our model was also tested by cross-correlations performed between the average patterns resulting from microneurographic recordings of Ia activities and the patterns generated by the proprioceptive model at ankle level.

Quantification of the kinesthetic illusions

The average shape of each sign drawn on the digitizing tablet was determined from all the trajectories. These trajectories were first normalized and then repositioned with a common starting point so that visual comparisons could be made. The criterion used to determine whether the participants recognized the illusory writing was correct identification of each symbol.

Drawing up vectors describing the various types of trajectories

Each of the four types of trajectories—Initial, Experimental, Model Ankle, and Model Wrist Trajectories—was also described by series of vectors giving the tangential velocity recorded during the same successive 200-ms time windows. To compare the direction and amplitude of each category of vectors, the vectors were normalized and the trajectory points used to construct them were sampled at 2-ms time steps.

| TABLE 1. Correlation between vectors describing the initial and modeled trajectories |
|-----------------------------------------------+---------------+---------------+---------------+---------------+---------------+---------------+---------------+----------------|
| Direction                                    | Letters       | Numbers       |               |
|                                              | a             | b             | e             | n             | 1             | 2             | 3             | 8              |
| Initial Trajectories/Modeled Trajectories    | 0.88          | 0.86          | 0.79          | 0.48          | 0.85          | 0.94          | 0.77          | 0.95           | 0.81          |
| Amplitude                                    | a             | b             | e             | n             | 1             | 2             | 3             | 8              | Average       |
| Initial Trajectories/Modeled Trajectories    | 0.90          | 0.91          | 0.91          | 0.71          | 0.92          | 0.95          | 0.80          | 0.83           | 0.87          |

Correlation coefficients were calculated for the ankle joint between vectors describing the Initial Trajectories (i.e., the movement trajectories imposed during microneurographic recordings and used to compute the patterns) and those describing the Modeled Trajectories, built up from the muscle spindle feedback generated by the model. Correlation coefficients were computed between the directions and the amplitudes of the various pairs of vectors.

RESULTS

Model validation: the recorded and modeled afferent patterns resembled each other

First of all, we tested the modeling procedure for the ankle joint. From the modeled patterns, we could deduce at each time point the population vectors representing the activity of each population of muscle afferents and then reconstruct the movement vectors by summing the population vectors. Then these population vectors were put head to tail to reconstruct a trajectory. This trajectory correlated with the corresponding Initial Trajectory used to compute the pattern. Table 1 gives the correlation coefficients between these two kinds of trajectories.

After including in the proprioceptive model the preferred sensory directions of each ankle muscle and calculating the instantaneous vectors describing the tangential velocity of the movement trajectories, it was possible to generate the afferent pattern emitted by each of the muscles activating the joint. The mean natural afferent patterns recorded microneurographically (blue traces) are compared in Fig. 3 with the patterns generated by the proprioceptive model (red traces) for movement trajectories forming the letter “a” and the number “8.” The frequency patterns were similar for both trajectories in most of the five ankle muscles. A highly significant level of correlation (0.82) was found between the natural and simulated patterns for several letters (a, b, e, n) and numbers (1, 2, 3, 8) in each of the five main ankle muscle groups. Only 4 of the 40 patterns studied gave a level of correlation <0.60 (see Table 2).

Recorded and modeled muscle spindle feedback patterns evoked similar illusory movements when used to pilot sets of vibrators

When the recorded and modeled afferent patterns were used to pilot a set of vibrators applied to the five main ankle muscle groups of motionless participants, all of them clearly perceived illusory foot-tip movements in both cases. The shapes of the illusory trajectories that the participants subsequently reproduced by hand on a digitizing tablet clearly resembled the outlines of various letters and numbers. Figure 4 gives the mean shapes of the trajectories drawn by all the participants. The averaged reproduced trajectories were very similar to those originally imposed on the foot, irrespective of whether recorded or modeled afferent patterns were used as the stimuli.

To analyze to what extent the spatiotemporal parameters of the two kinds of perceived illusory movements paralleled those of the imposed movements, correlation analyses were carried out on the direction and the amplitude of each group of vectors.
Table 3 gives the correlation coefficients obtained when comparing the kinematic parameters of the Initial Trajectories with those of the Experimental Illusory Trajectories and Model Ankle ones. The mean correlation coefficients obtained were \( r_{\text{dir}} \) 0.85 and \( r_{\text{amp}} \) 0.90 in the first case and \( r_{\text{dir}} \) 0.84 and \( r_{\text{amp}} \) 0.91 in the second case. In addition, the illusory movements induced by applying the Experimental and the Model Ankle patterns resembled each other, as shown by the mean correlations obtained, i.e., \( r_{\text{dir}} \) = 0.86 and \( r_{\text{amp}} \) = 0.89 (third line).

The proprioceptive model can be applied to different joints and to any virtual two-dimensional movements

To check the effectiveness of the proprioceptive model with other joints, it was tested at wrist level. First, the values of the preferred directions of the four wrist muscle groups were included in the model. Second, we generated afferent patterns corresponding to trajectories previously imposed on the foot and to eight new trajectories: two letters (u and v), two numbers (6 and 9), and four geometrical shapes (rectangle, square, triangle, and circle). Here again, the participants were asked to actively draw the illusory movements they perceived on a digitizing tablet. Correlation analyses (see Table 4) showed that the kinematic parameters of the Initial Trajectory and the Model Wrist Trajectory matched (\( r_{\text{dir}} \) = 0.82; \( r_{\text{amp}} \) = 0.86).

Figure 4 shows the similarities between the trajectories initially drawn on the digitizing tablet and the corresponding mean illusory trajectories induced at hand level using the modeled vibration patterns. High correlations were also found with the new trajectories tested at the wrist level (see Table 4). Finally, participants were also able to recognize the illusory trajectories in terms of graphic symbols. Indeed, before copying the illusory movements they perceived on a digitizing tablet, the participants were asked to name the letters, numbers, and geometrical figures formed by the illusory movement trajectories they perceived. Table 5 gives the recognition rates recorded under all the experimental conditions tested. The participants identified the symbols correctly in three quarters of the trials and there were no striking differences between foot and hand level or between the illusory movements induced by recorded afferent patterns and those generated by the proprioceptive model.

### Table 2. Correlation between the natural afferent patterns recorded microneurographically and the artificial patterns generated by the proprioceptive model

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Letters</th>
<th>Numbers</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>TA + EHL</td>
<td>0.82</td>
<td>0.74</td>
</tr>
<tr>
<td>EDL</td>
<td>0.73</td>
<td>0.79</td>
</tr>
<tr>
<td>PL</td>
<td>0.77</td>
<td>0.61</td>
</tr>
<tr>
<td>GS</td>
<td>0.71</td>
<td>0.84</td>
</tr>
<tr>
<td>TP</td>
<td>0.86</td>
<td>0.89</td>
</tr>
<tr>
<td>Average</td>
<td>0.78</td>
<td>0.79</td>
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</table>

Correlation coefficients for various letters (a, b, c, n) and numbers (1, 2, 3, 8) in each of the five main ankle muscle groups (TA, tibialis anterior; EHL, extensor hallucis longus; EDL, extensor digitorum longus; PL, peroneus lateralis; GS, gastrocnemius soleus; and TP, tibialis posterior muscles). NaN, not a number.
TABLE 3. Correlation coefficients between vectors describing imposed and illusory ankle movements

<table>
<thead>
<tr>
<th>Direction</th>
<th>Letters</th>
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<tbody>
<tr>
<td></td>
<td>a</td>
<td>b</td>
<td>c</td>
<td>n</td>
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<td>2</td>
<td>3</td>
<td>8</td>
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<tr>
<td>Initial Trajectories/Experimental</td>
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<td>0.74</td>
<td>0.99</td>
<td>0.93</td>
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<td>0.79</td>
<td>0.91</td>
<td>0.80</td>
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<tr>
<td>Initial Trajectories/Model Ankle</td>
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<td>0.68</td>
<td>0.93</td>
<td>0.90</td>
<td>0.90</td>
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<td>0.84</td>
<td>0.84</td>
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<tr>
<td>Experimental/Model Ankle</td>
<td>0.88</td>
<td>0.79</td>
<td>0.94</td>
<td>0.91</td>
<td>0.88</td>
<td>0.84</td>
<td>0.86</td>
<td>0.83</td>
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<td>Amplitude</td>
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<td></td>
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Vectors describing imposed movement trajectories (labeled “Initial Trajectories”) and those describing the illusory trajectories induced using either the recorded afferent patterns (labeled “Experimental”) or the simulated afferent patterns (labeled “Model Ankle”) at the ankle level with different letters (a, b, c, n) and numbers (1, 2, 3, 8). Correlation coefficients were computed between the directions and the amplitudes of the various pairs of vectors.


discussion

We chose to build our proprioceptive model according to the functional properties of Ia afferent populations revealed through recordings on humans performing movements. This model accurately generates complex vibratory patterns, whose frequencies mimic almost exactly those of the muscle spindle feedback evoked by actual movements. These modeled vibratory patterns can be applied to sets of muscles to elicit virtual two-dimensional movements. Another important feature of our model is that it can be adapted to other joints if one specifies, for a given posture, the preferred sensory direction of each muscle group acting at a joint.

From movement trajectory to the corresponding proprioceptive afferent feedback

The complex multimuscle proprioceptive coding of the spatial and kinematic parameters of any movement trajectory can be described by a population vector model under both passive and active conditions at both hand and foot levels (Albert et al. 2006; Bergenheim et al. 2000; Jones et al. 2001; Roll et al. 2004). Interestingly, this suggests that some general neuronal coding principles previously found to pertain at the motor cortical level responsible for motor command in monkeys (Caminiti et al. 1990; Georgopoulos et al. 1984; Johnson and Ebner 2000; Kalaska 1991; Schwartz and Moran 1999, 2000; Schwartz et al. 1988) may also be relevant at the sensory level. At these motor and sensory levels, this principle states that, at any point on a movement trajectory, the computed neural sum vector fits well with the ongoing movement vector describing the trajectory.

The adaptation by Bergenheim et al. (2000) of this “central population vector model” to the sensory level requires considering the anatomical and physiological organization of the muscular system. In particular, the sensory receptors merge into a homogeneous population inside the muscle that bears them (see Bergenheim et al. 2000; Fig. 4). Since all the sensory receptors inside a muscle have an extremely close Preferred Sensory Direction, this feature allows one to compute, for a population of receptors, only one Preferred Sensory Direction for a given muscle. Although the number of vectors to be summed was limited and all the directions were not equally represented, our proprioceptive model is highly effective, especially in view of the high correlation between the Initial Trajectories and the trajectories reconstructed from the modeled afferent patterns.

The instantaneous neurosensory sum vector corresponds to the sum of all the “population vectors” giving the weighted and oriented contribution of the afferent feedback of each muscle to the sensory coding of movement direction and velocity (Bergenheim et al. 2000; Ribot-Ciscar et al. 2002; Roll et al. 2000, 2004). Since the instantaneous tangent vectors describing the trajectory correlate with the corresponding neurosensory sum vectors (Albert et al. 2005, 2006; Roll et al. 2004), our modeling consists in following the procedure backward: each sum vector is decomposed into a series of population vectors

TABLE 4. Correlation coefficients between vectors describing imposed and illusory wrist movements

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<tr>
<td>Model Ankle/Model Wrist</td>
<td>0.68</td>
<td>0.79</td>
<td>0.93</td>
<td>0.77</td>
<td>—</td>
<td>—</td>
<td>0.82</td>
<td>0.75</td>
<td>0.79</td>
<td>—</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>6</td>
<td>8</td>
</tr>
<tr>
<td>Initial Trajectories/Model Wrist</td>
<td>0.74</td>
<td>0.84</td>
<td>0.97</td>
<td>0.85</td>
<td>0.84</td>
<td>0.88</td>
<td>0.85</td>
<td>0.85</td>
<td>0.88</td>
<td>0.89</td>
<td>0.91</td>
</tr>
<tr>
<td>Model Ankle/Model Wrist</td>
<td>0.73</td>
<td>0.80</td>
<td>0.96</td>
<td>0.84</td>
<td>—</td>
<td>—</td>
<td>0.85</td>
<td>0.80</td>
<td>0.86</td>
<td>—</td>
<td>0.89</td>
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</table>

Shown are vectors describing imposed movement trajectories (labeled “Initial Trajectories”) and those describing the illusory trajectories induced using the afferent patterns simulated at the ankle level (labeled “Model Ankle”) and at the wrist level (labeled “Model Wrist”) with various letters (a, b, c, n, u, v), numbers (1, 2, 3, 6, 8, 9), and geometrical shapes (square, circle, rectangle, triangle). Correlation coefficients were calculated on the directions and the amplitudes of the various pairs of vectors. Note that no correlation coefficients are given for the letters “u” and “v”; the numbers “6” and “9”; or the four geometrical shapes studied (square, circle, rectangle, triangle) between the ankle and wrist levels because these eight new trajectories were tested only at the wrist level.
giving the mean discharge frequency of the afferents in each muscle at any moment. In addition, the mean instantaneous firing rate of each muscle spindle population is a cosine function of the difference between the direction of the trajectory and the preferred sensory direction of the muscle (Bergenheim et al. 2000). The proprioceptive model therefore generates the mean afferent patterns produced by each of the muscles surrounding a given joint during a two-dimensional movement trajectory. This was confirmed by the high correlations between the firing frequencies in the recorded and modeled afferent patterns.

In behavioral conditions, muscle spindle feedbacks evoked by the performance of two-dimensional movements forming letters or numbers were previously found to be specific to each trajectory and perfectly reproducible when the same movement was repeated (Albert et al. 2006; Roll et al. 2004). For a given joint, the mean afferent feedback pattern can be determined as a specific firing pattern, in which any increase in the frequencies corresponds to the stretching phases of the receptor-bearing muscles. If all the sensory activities of the muscles involved are taken together, one obtains what we have called the “proprioceptive signature” of a given movement (Roll et al. 2004).

So this model constitutes a real methodological breakthrough, in that it gives access to these “proprioceptive signatures” evoked in humans by the execution of any two-dimensional movement. The only method available so far for this purpose was the microneurographic method, a very demanding and rather invasive procedure (Bergenheim et al. 1999; Vallbo and Hagbarth 1968).

Both the recorded and modeled proprioceptive patterns induced similar virtual two-dimensional movements

Since the afferent patterns generated by the model closely paralleled those recorded in participants during actual movements, it was expected that using these two types of patterns to pilot the set of vibrators would give rise to fairly similar illusory movements. Before using the afferent patterns to pilot a set of vibrators, it was first necessary to check the validity of the method. In a recent study, we investigated whether an afferent pattern previously recorded during an actual movement gave rise to a similar afferent pattern when reapplied to a muscle tendon via vibration. The two firing patterns were in fact practically identical (Albert et al. 2006; Fig. 2). In addition, the illusory trajectories induced at the ankle level using the two types of afferent patterns were very similar in terms of the resulting shape and the instantaneous tangential velocity (Albert et al. 2005).

When the proprioceptive model was applied to the wrist after specifying the preferred sensory direction of each wrist muscle group, the illusory trajectories induced at hand level were also similar to those evoked at the ankle level. This finding confirms that the model can be used to generate virtual writing or drawing movements with various two-dimensional trajectories at various joints.

The muscle spindle afferent patterns recorded and the modeled patterns applied via vibration gave rise to illusory trajectories forming symbols (letters, numbers, and geometrical shapes) that were in both cases equally well recognized by the participants. This point was checked by asking the participants to name the letter, number, or geometrical figure formed by the perceived illusory trajectory before copying it on the digitizing tablet. No significant differences were observed between the recognition rates obtained by the participants when natural versus modeled afferent patterns were used (~75%). To determine how meaningful this ratio is, especially when the participants had to recognize writing movements that did not correspond to their own cursive writing, we compared it with the recognition ratio (91%) when passively imposing the same movements to the ankle of 10 subjects (F. Albert, C. Thyron, and J. P. Roll, unpublished observations).

Last, either for the active copy of a movement perceived by a participant or its symbolic identification, one could question the relevance of studying such standard and overlearned trajectories instead of more abstract shapes. The question arises as to whether the participants reproduced their own writing or drawing movement or carefully copied the illusory trajectories they perceived. As reported by Albert et al. (2006) in Fig. 3C the participants did not reproduce their own usual handwriting; rather, they reproduced illusions of movement they perceived while they were exposed to vibration. This was particularly obvious for the number “8,” for which both the imposed and reproduced trajectories started with an upward movement to the left, whereas the usual writing trajectory of some of the participants started with a downward movement to the left. Further proof is brought by the lower correlation coefficients

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**TABLE 5. Recognition rates of graphic symbols**

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>b</th>
<th>e</th>
<th>n</th>
<th>Average (Letters)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model Ankle</td>
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<td>90</td>
<td>90</td>
<td>80</td>
<td>80</td>
</tr>
<tr>
<td>Model Wrist</td>
<td>30</td>
<td>80</td>
<td>80</td>
<td>60</td>
<td>63</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>8</td>
<td>Average (Numbers)</td>
</tr>
<tr>
<td></td>
<td>90</td>
<td>70</td>
<td>80</td>
<td>70</td>
<td>78</td>
</tr>
<tr>
<td>Model Ankle</td>
<td>90</td>
<td>60</td>
<td>90</td>
<td>70</td>
<td>78</td>
</tr>
<tr>
<td>Model Wrist</td>
<td>80</td>
<td>60</td>
<td>80</td>
<td>90</td>
<td>78</td>
</tr>
</tbody>
</table>

Mean rate of correct identification (recognition rate) of the graphic symbols tested in each experimental condition (A) and the new trajectories tested only at the wrist level (B).
between the vectors describing the reproduced and the usual handwriting trajectories (Albert et al. 2006; Table 1).

These observations confirm the validity of the present method that uses symbolic illusory movements. Indeed, these movements can be recognized solely on the basis of proprioceptive afferent inputs (Albert et al. 2005, 2006; Roll et al. 1996; Viviani et al. 1997), even if other sensory modalities certainly contribute to the recognition process in natural behavior (Bara et al. 2004; Collins and Prochazka 1996; Gordon and Soechting 1995). To conclude, our proprioceptive model, which is directly based on neurosensory data recorded in behaving humans, can be used to generate the complex proprioceptive feedback patterns associated with the execution of any two-dimensional movement. Its simplicity and accuracy as a means of inducing virtual two-dimensional movements in motionless participants make it a potentially valuable tool for use in fields of research such as sensorimotor learning, patient rehabilitation, and virtual reality.

GRANTS

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Goodwin GM, McInnes DJ, Matthews PB. The contribution of muscle afferents to kinaesthesia shown by vibration induced illusions of movement and by the effects of paralyzing joint afferents. Brain 95: 705–748, 1972.


