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RESEARCH ARTICLE

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From balance regulation to body orientation: two goals for muscle proprioceptive information processing?

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Abstract This study was based on the assumption that the central processing of proprioceptive inputs that arise from numerous muscles contributes to both awareness and control of body posture. The muscle-spindle inputs form a "proprioceptive chain" which functionally links the eye muscles to the foot muscles. Here, we focused on the specific contribution of two links in the control of human erect posture by investigating how proprioceptive messages arising from ankle and neck muscles may be integrated by the central nervous system. Single or combined mechanical vibrations were applied to different muscle tendons at either one (ankle or neck) or both (ankle plus neck) body levels. The amplitude and the specific direction of the resulting oriented body tilts were analyzed by recording the center of foot pressure (CoP) through a force platform with four strain gauges. The results can be summarized as follows: (1) the vibration-induced whole-body tilts were oriented according to the muscles stimulated; furthermore, the tilts were in opposite directions when neck or ankle muscles on the same side of the body were stimulated; (2) except for the ankle antagonist muscles, co-vibrating adjacent or antagonist muscles at the same body level (ankle or neck) resulted in body sways, whose orientation was a combination of those obtained by stimulating these muscles separately; and (3) likewise, co-vibrating ankle and neck muscles induced whole-body postural responses, whose direction and amplitude were a combination of those obtained by separate vibration. We conclude that the multiple proprioceptive inputs originating from either one or both body levels may be co-processed in terms of vector-addition laws. Moreover, we propose that proprioceptive information from ankle and neck muscles may be used for two tasks: balance control and body orientation, with central integration of both tasks.

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Introduction

Previous ideas about the organization and control of human erect posture have been considerably revised during the last decade. The idea of an "internal model" has been added to the traditional assumption that postural activities basically depend on interactions between "single level reflexes" (Sherrington 1906). This model is thought to operate with highly integrated multi-sensory information and to deal much more adaptively and flexibly with a wide range of tasks (Gurfinkel et al. 1988; Horak and MacPherson 1996; Massion 1992; Merfeld et al. 1993). For example, the perceptual or motor responses after muscle vibration can involve either the whole-body or a single segment, depending on the instructions given to the subjects or their environment (Quoniam et al. 1990; Roll et al. 1986). The "postural body scheme", considered to be an unconscious representation of the body's configuration and dynamics, may form a reference frame, which the central nervous system uses to continuously restore the body's balance or its required orientation (Clément et al. 1984; Gurfinkel et al. 1988, 1995; Lestienne and Gurfinkel 1988).

On these lines, postural control is approached not only in terms of an automatic regulative process for the maintenance of the body equilibrium, but also in terms of a high-level process, including body spatial representation. In fact, every directed activity in extrapersonal space implies that the body was previously oriented (Gurfinkel and Levick 1991). As pointed out by Horak and MacPherson (1996), posture seems to subserve two behavioral goals: orientation and balance.

Visual, vestibular, cutaneous, and muscle proprioceptive sensory modalities (Fetter and Dichgans 1996; Horak and Shupert 1994) are involved in postural control. Muscle proprioceptive information seems to play a major role, since it arises from receptors distributed throughout the body. In particular, the representation of the body's static and dynamic geometry might be largely based on muscle proprioceptive inputs that continuously inform the central nervous system about the position of each part of the body in relation to the others (Massion 1992; Roll et al. 1989b).

Eklund (1972) established that oriented whole-body tilts could be induced in standing human subjects by applying vibratory stimulation to the ankle postural muscles: stimulating the tibialis anterior muscles results in a forward tilt and stimulating the triceps surae muscles causes a backward tilt. Other muscles have been investigated: paravertebral (Gregoric et al. 1978; Smetanin et al. 1993), cervical (Gurfinkel et al. 1988; Lund 1980; Roll and Roll 1988), and extraocular (Roll and Roll 1987). In all these cases, the induced postural responses are oriented in specific directions, depending on the vibrated muscle. Therefore, Roll and Roll (1988) have suggested that muscle-spindle inputs might form a continuous "proprioceptive chain" from the feet to the eyes, since applying tendon vibration at any level in the chain apparently alters the internal representation of the body posture. Little is known, however, about how this multiple proprioceptive information is integrated.

It is known that the proprioceptive messages arising from various muscles are centrally integrated for perceptual purposes, since applying various spatio-temporal patterns of vibration to the wrist muscles evokes quite complex illusions of movement, for instance, when one draws geometrical figures (Roll and Gilhodes 1995; Roll et al. 1996). The latter authors suggested that the perceptual integration of the multiple proprioceptive inputs may obey vector combination rules.

We attempted to investigate whether and how the processing of proprioceptive messages arising from the neck or ankle or both might be involved in the organization and maintenance of body posture. In particular, we focused on the laws governing the sensorimotor integration processes subserving human postural control. In a first experiment, adjacent or antagonist muscles at the neck and ankle levels were vibrated either separately or together, and the corresponding postural responses were analyzed. In a second experiment, the stimulation was applied concomitantly at both body levels to determine to what extent the various links in the proprioceptive chain are functionally inter-dependent in postural control.

Materials and methods

Subjects

Two experiments on two groups of healthy subjects, each including six men and five women (age range: 22–55 years old), were performed with the approval of the local Ethics Committee. All the participants gave their informed consent to the experimental procedure as required by the Helsinki declaration (1964).

Experimental set-up

In all experiments, the subject was placed on a force platform. Antero-posterior and lateral displacements of the center of pressure (CoP) exerted by the subject's feet were recorded by four transducers in the force platform. Proprioceptive stimulation was delivered by four mechanical vibrators, which consisted of biaxial DC motors equipped with small excentric masses. They were attached to the subject's ankle or neck by elastic bands. The tendons of various muscle groups at these two body levels were stimulated at a set vibration frequency (80 Hz) and amplitude (0.2–0.4 mm, peak to peak). When several muscle groups were co-vibrated, the vibration onsets were synchronized and the stimulation durations were identical.

Procedure

Under each experimental condition, the subjects were asked to stand erect on the force platform with their feet parallel, their eyes closed, and their hands at their sides. They were instructed to relax and not to resist any vibration-induced body tilts. They were promised that, if need be, one of the experimenters would prevent them from falling during the experiments. The various vibration conditions applied are shown in the form of pictograms (Fig. 1).

Experiment 1

Subjects were tested under sixteen conditions of stimulation, each consisting of two trials, except for the control condition, in which no vibration was applied. The vibratory stimulation lasted for 3 s. The data were recorded in each trial during a period of 8 s, including 1 s before vibration onset and 4 s after the vibration was stopped. At each body level (neck or ankles), two separate blocks of eight trials were run, one with single and the other with combined muscle group vibration.

Single muscle-group vibration

"Single" vibratory stimulation refers to vibratory stimulation applied to the same side of either the neck or the two ankles. At the cervical level, vibratory stimulation was successively applied to the anterior, posterior, right, or left parts of the neck, i.e., the sternocleidomastoidus, splenius, right, or left trapezius muscles. At the ankle level, vibration was always applied bilaterally to the same muscle groups of both legs: that is, to the two tibialis anterior or two soleus muscles; moreover, when the stimulation was applied laterally, it was always applied simultaneously to the peroneus lateralis of one leg and to the tibialis posterior of the other leg.

Combined "adjacent" muscle-group vibration

"Combined" means vibratory stimulation simultaneously applied to two sides of either the neck or the two ankles. "Adjacent" co-vibration refers to the eight conditions of stimulation in which vibration was applied simultaneously to two muscle groups, one with an antero-posterior and the other with a lateral insertion. At the cervical level, we therefore tested the effects of four different patterns of co-stimulation, in which vibration was applied to either the sternocleidomastoidus or splenius muscles and, concomitantly, to either the right or left trapezius muscles. Concurrently, at the ankle level, the tibialis anterior or soleus muscles were co-stimulated with the right tibialis posterior and left peroneus lateralis muscles or with the left tibialis posterior and right peroneus lateralis muscles.

Experiment 2

This experiment consisted of ten automatically averaged trials run under each of ten conditions of stimulation. Here, the data were re-

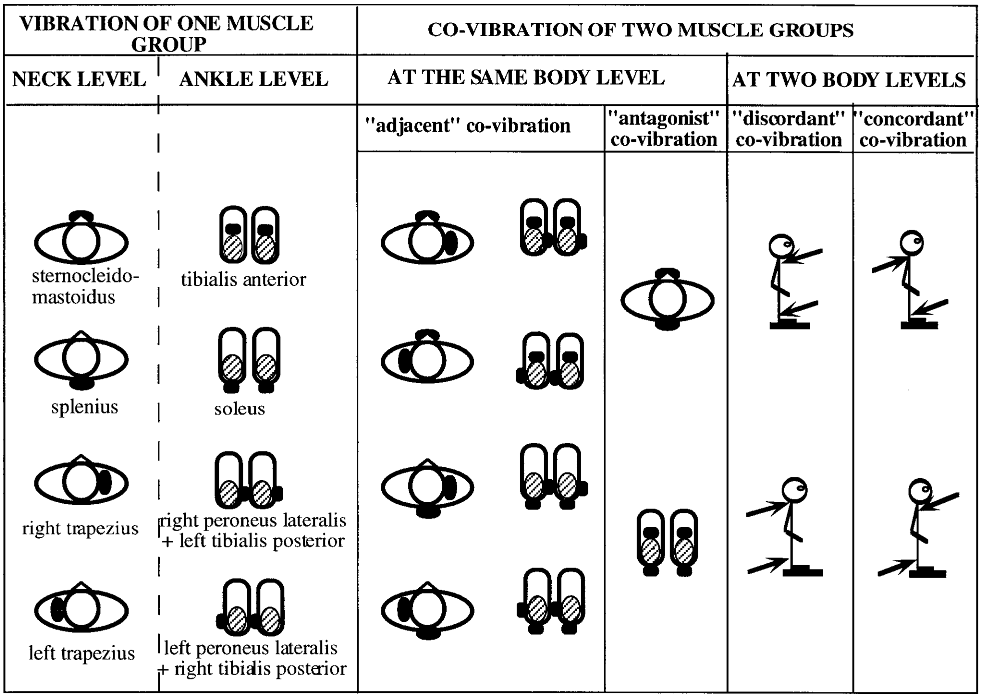

Fig. 1 Summary of the various vibration conditions applied to one or two muscle groups, either at the same level (neck or ankle) or at two levels (neck plus ankle). The *black points* and *arrows* indicate the vibration sites and the vibrators

corded for 3 s. The stimulus of 2-s duration occurred 500 ms after the beginning of the trial. Four control conditions were first tested, in which single muscle-group vibration was applied to the anterior or posterior sides of the ankles and the neck. Six complementary, combined co-vibration conditions were then run, involving two anterior and posterior muscle groups at either the same or both body levels.

Combined muscle-group vibration at the same body level

Two intra-level patterns of co-stimulation were used, involving antagonist muscle groups, i.e., either the sternocleidomastoidus and splenius muscles at the cervical level or the tibialis anterior and soleus muscles of both legs at the ankle level.

Combined muscle-group vibration at both body levels

The effects of four inter-level patterns of co-stimulation were tested. Two "concordantly" acting patterns of co-vibration, involving two muscle groups which, when separately stimulated, resulted in body displacements in the same direction. This was the case with the sternocleidomastoidus and the two soleus muscles on the one hand and with the splenius and the two tibialis anterior muscles on the other hand. Conversely, two "discordantly" acting patterns of co-vibration, involving two muscle groups which, when separately stimulated, resulted in postural responses in opposite directions. This was the case with the sternocleidomastoidus and the two tibialis anterior muscles on the one hand and with the splenius and the two soleus muscles on the other hand.

Data analysis

The CoP coordinates were recorded at a sampling rate of 25 Hz. The results are expressed in terms of all subject's mean shift (in mm) of CoP in relation to the mean initial position prior to the vibration onset. Under all experimental conditions, every subject's CoP position in the horizontal plane (X–Y mean amplitudes) was recorded after 2 s of vibration, i.e., before the experimenter had to prevent the subjects from falling. Confidence ellipses centered on the bivariate mean of these CoP positions were calculated in order to show the 95% confidence limits for the mean of the reference population (Batschelet 1981).

To analyze the possible additive effects of the co-vibration of two muscle groups, vectors were drawn to show the degree of agreement between the mean experimental vector and the expected one. The mean experimental vector was defined in polar coordinates that corresponded to both the direction and amplitude of the mean CoP shift after 2 s of co-vibration. The theoretical vector resulted from the vectorial sum of the two mean isolated vectors obtained when vibration was applied separately to each of these two muscle groups.

Under each co-stimulation condition of the two experiments, we tested, by the v-test (Batschelet 1981; Zar 1996), whether the direction of the experimental vectors (α_i) for all subjects (i=1, ...11) was randomly distributed over a circle or had a significant tendency to cluster around the theoretical one (α_i'). For this purpose, every subject's angular deviation (ϕ_i) with respect to the direction defined by the theoretical vector was calculated. The distribution of angular deviations ϕ_i was first statistically summarized by a mean vector, whose direction ϕ_m expressed the angular mean of the distribution, and the length R_m (ranging between 0 and 1) expressed the concentration of the distribution around the angular mean:

$$\phi_i = \alpha_i - \alpha_i'$$

$$C = 1/n^* \Sigma \cos\phi_i$$

$$S = 1/n^* \Sigma \sin\phi_i$$

$$R_m = \sqrt{(C^2 + S^2)}$$

$$\phi_m = \arctan(S/C) + k^* 180^\circ,\ \text{with}\ k = 0\ \text{if}\ C > 0\ \text{and 1otherwise.}$$

The "v" value was obtained by multiplying the length of the mean vector by the cosine of the angular mean: $v = R_m * \cos(\phi_m)$. Thus, if the directions of the experimental vectors (α_i) did not differ much from the expected values (α_i'), "v" was close to one. Otherwise, "v" was considerably smaller than one, i.e., the angular deviations were either uniformly distributed over a circle or clustered in a direction different from that of the theoretical vector. Moreover, using Student's paired *t*-test, we compared the length of the mean experimental vector with that of the theoretical vector. In this test, all the experimental data, expressed in percent with respect to the theoretical values, were compared with the reference value equal to 100%.

Results

Postural effects of neck- or ankle-muscle vibration

Single muscle-group vibration

At both body levels, applying vibratory stimulation to muscle groups with an antero-posterior or lateral insertion led to orthogonally oriented whole-body tilts, i.e., in the antero-posterior and lateral directions, respectively (Fig. 2A, B).

Neck-muscle vibration had consistent postural effects: the resulting body sway was always in the contralateral direction with respect to the vibrated muscle site, i.e., backwards in response to stimulation of the sternocleidomastoidus muscles and forwards in response to stimulation of the splenius muscles (Fig. 2A). Conversely, ankle-muscle vibration gave rise to postural responses oriented ipsilaterally with respect to the vibrated muscle. A forward body sway occurred in response to stimulation of the two tibialis anterior muscles and a backward one in response to stimulation of the two soleus muscles (Fig. 2B).

Whatever the body level tested, the mean amplitudes of the CoP shifts were variable. In particular, the forward-directed responses were on average greater in amplitude (Y=56.7±25.7 mm with ankle vibration; Y=59±19.9 mm with neck vibration) than the backward-directed responses (Y=–36.8±23.9 mm with ankle vibration; Y=–34.3±18.2 mm with neck vibration).

Co-vibration of two "adjacent" muscle groups

When one antero-posterior muscle group was stimulated together with one lateral muscle group, an obliquely oriented body sway was always induced. It corresponded roughly to the sum of the two orthogonal body sways previously observed in response to stimulating these same muscles separately. For example, Fig. 3A shows that the body tilt resulting from co-vibrating the splenius and left trapezius muscles was directed forward and to the right, whereas, as shown in Fig. 2A, vibrating the splenii separately tilted the body forward and vibrating the left trapezius shifted it to the right. The responses to the other combined stimulations applied to either neck (Fig. 3A) or ankle muscle groups were all as above.

To determine whether the postural response induced by co-vibrating each pair of adjacent muscle groups at the ankle or neck levels was the sum of the two singly induced effects, we compared the mean experimental vector with the theoretical one. The mean experimental vector corresponded to the direction and the amplitude of the CoP shift after 2 s of co-vibration, and the theoretical vector resulted from the vectorial sum of the two mean orthogonal vectors obtained upon vibrating each of these same muscles separately. As an example, Fig. 3B shows the results of co-vibration applied to the splenius and left trapezius muscles. In this case, the mean experimental vector was in the close vicinity of the theoretical vector resulting from the vectorial sum of the two orthogonal vectors (v-test, $P<0.0001$).

This result was observed for all the other "adjacent" co-vibration conditions. The polar coordinates of the mean experimental (direction α_m±SD; length r_m±SD) and theoretical ($\alpha'_m \pm$ SD; $r'_m \pm$ SD) vectors under each condition in which "adjacent" co-stimulation was applied are given in Table 1 (neck) and 2 (ankle). In all cases, the direction of the experimental responses had a significant (v-test, $P<0.001$) tendency to cluster around the direction of the theoretical ones. Moreover, no significant difference was found between the lengths of the mean experimental and theoretical vectors (*t*-test, $P>0.05$).

Co-vibration of two antagonist muscle groups

At the two body levels, the simultaneous vibration of two anterior and posterior antagonist muscle groups cancelled

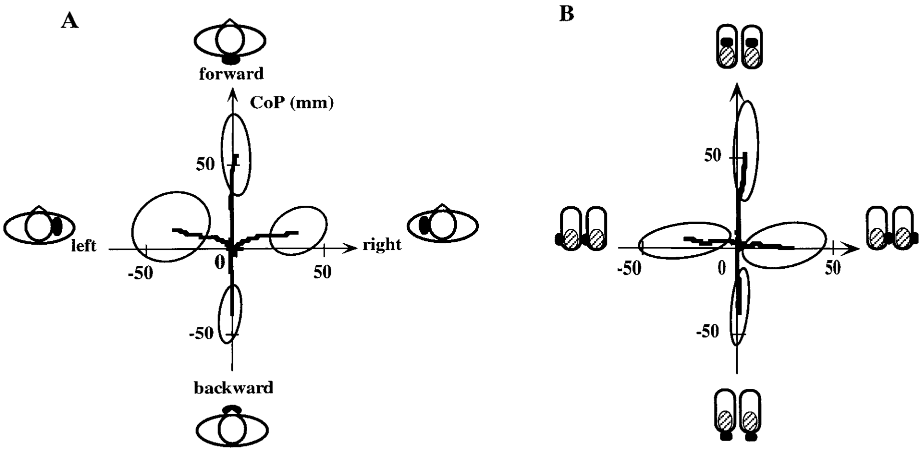

Fig. 2 Mean oriented postural responses induced by applying vibratory stimulation to a single muscle group at the neck (**A**) or ankle (**B**) level. *Traces* are the mean trajectories (statokinesigrams) of the center of foot pressure (CoP). The *confidence ellipses,* centered on the bivariate mean of the CoP positions after 2-s vibration, show the 95% confidence limits for the mean of the reference population. The *pictograms* beside the posturographic recordings indicate the vibration sites

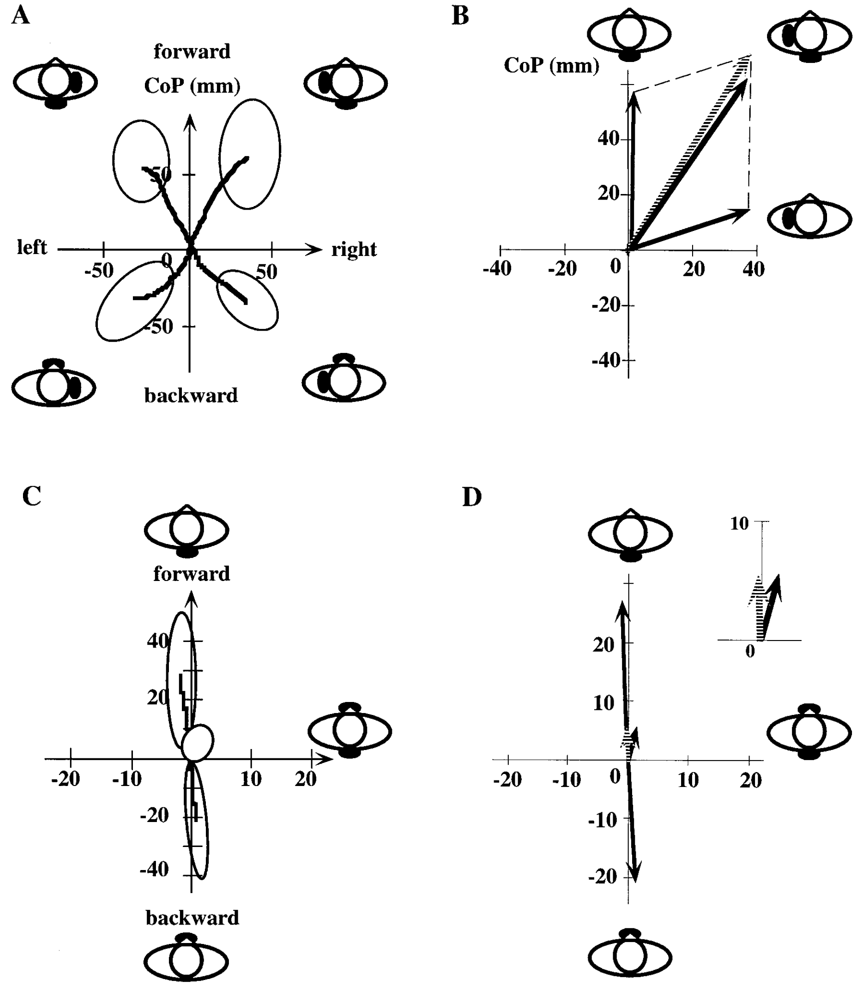

Fig. 3 **A, B** Mean postural responses induced by co-vibrating two "adjacent" muscle groups at the neck level. **C, D** Mean postural reponses induced by co-vibrating two antagonist muscle groups at the neck level. *Traces* are the mean trajectories (statokinesigrams) of the center of foot pressure (CoP). The *confidence ellipses*, centered on the bivariate mean of the CoP positions after 2-s vibration, show the 95% confidence limits for the mean of the reference population. The *pictograms* beside the posturographic results indicate the vibration sites. *Mean vectors* give the direction and amplitude of the postural responses induced by vibrating the splenius and left trapezius (**B**) or the sternocleidomastoidus and splenius muscles (**D**) separately or concomitantly. *Bold arrows* Mean experimental vectors, *hatched arrows* theoretical vectors corresponding to the vectorial sum of the two mean experimental vectors obtained when the two muscle groups were stimulated separately. Note the exact fit between the mean experimental and theoretical vectors

the postural effects in opposite directions observed with separate stimulation. Indeed, such co-vibration resulted, in all cases, in very small amplitude of the CoP shifts. Figure 3C and D show that, at the cervical level, the length of the mean experimental vector corresponding to the co-vibration of the sternocleidomastoidus and splenius muscles (r_m=6.3±5.5 mm) did not differ significantly (*t*-test, P>0.7) from the length of the theoretical vector (r'_m =9.5±5.7 mm). In addition, the direction of the experimental postural response was significantly close to the expected one (v-test, P<0.05).

At the ankle level, however, the postural response upon co-vibrating the tibialis anterior and soleus muscles was not equal to the sum of the mean effects upon vibrating these two muscle groups separately. The length of the mean experimental vector (r_m=8±6.3 mm) was significantly smaller (*t*-test, P<0.05) than the predicted value (r'_m =26.6±16.5 mm), and the experimental direction (α_m=181°±83) was significantly different (v-test, P>0.05) from the predicted value (α'_m =117°±72).

Postural effects of neck- and ankle-muscle co-vibration

"Discordantly" acting co-vibration applied to muscle groups at both the neck and ankle levels

Similarly to when antagonist co-stimulation was applied at a single body level, the amplitudes of postural shifts were very small upon co-stimulating two muscle groups at different body levels, which, when stimulated separately, induced postural responses in opposite directions (Fig. 4A). Moreover, under the two "discordant" conditions, the length of each mean experimental vector did not differ significantly (*t*-test, P>0.05) from that of the theoretical vector. Elsewhere, the directions of the experimental vectors had a significant tendency (v-test, P<0.05) to cluster around the expected values.

"Concordantly" acting co-vibration applied to muscle groups at both the neck and ankle levels

Upon co-vibrating two muscle groups at different body levels, which, when stimulated separately, gave rise to body tilts in the same direction, the body sway continued

Tables 1, 2 Comparison of the polar coordinates (direction ±SD; length ±SD) of the mean experimental vectors (α_m; r_m) corresponding to center-of-foot-pressure (CoP) shifts after applying vibration simultaneously for 2 s to two adjacent muscle groups (*Exp*) and the calculated theoretical (*Theo*) mean values (α'_m; r'_m). The results of both *v-tests* and Student's paired *t-tests* are given in each case of "adjacent" co-vibration conditions. The *pictograms* indicate the co-vibration sites

Table 1 Results for "adjacent" co-vibration applied at the neck level

								
	Exp	Theo	Exp	Theo	Exp	Theo	Exp	Theo
$\alpha_m \alpha'_m$(°)	228±20	245±101	314±14	321±28	121±21	119±19	58±17	62±8
v-test (*P*)	*P*<0.0001		*P*<0.0001		*P*<0.0001		*P*<0.0001	
$r_m r'_m$(mm)	49.4±26.2	56.1±20.3	49.3±20.6	49.5±12.8	66.6±20.6	84.1±27.2	74.2±28.4	76.4±30.6
t-test (*P*)	0.21		0.95		0.08		0.61	

Table 2 Results for "adjacent" co-vibration applied at the ankle level

								
	Exp	Theo	Exp	Theo	Exp	Theo	Exp	Theo
$\alpha_m \alpha'_m$(°)	53±20	60±26	125±12	118±20	305±27	316±31	238±19	233±23
v-test (*P*)	*P*<0.0001		*P*<0.0001		*P*<0.001		*P*<0.001	
$r_m r'_m$(mm)	55.7±26.4	69.9±18.9	62.6±30.1	65.1±16.8	37.3±26.4	51.8±26.7	50.5±25.7	52.4±34.4
t-test (*P*)	0.22		0.89		0.06		0.44	

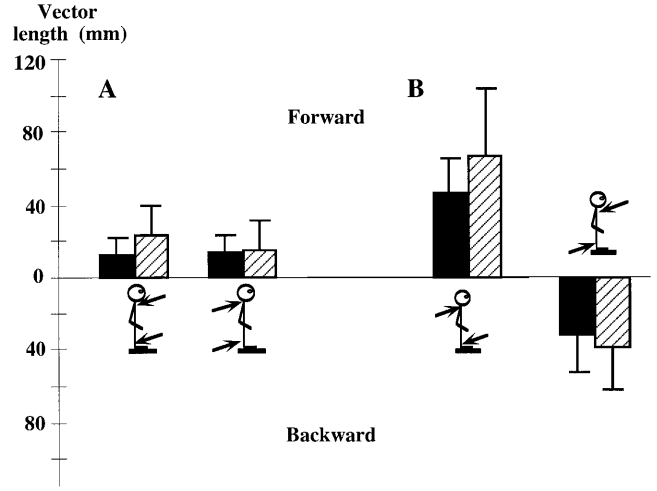

Fig. 4A, B Comparisons of the observed and expected amplitudes of the mean postural responses induced by applying vibratory co-stimulation to two muscle groups at both the neck and ankle levels. *Black histograms* give the length (±SD) of the mean experimental vectors corresponding to the center-of-foot-pressure (CoP) shifts in response to combined inter-level vibration applied to two muscle groups. *Hatched histograms* give the length (±SD) of the theoretical vectors resulting from the vectorial sum of the mean isolated vectors corresponding to the CoP shifts in response to vibrations applied separately to each of the two muscle groups. **A** Mean postural responses induced by "discordant" co-vibration: the tibialis anterior and sternocleidomastoidus muscles, soleus and splenius muscles. **B** Mean postural responses induced by "concordant" co-vibration: the tibialis anterior and splenius muscles, soleus and sternocleidomastoidus muscles

to occur in this same direction. For example, co-vibrating the tibialis anterior and splenius muscles led to a forward body sway, as did vibrating each of these muscles separately (Fig. 4B). In fact, the directions of the postural responses induced under both "concordant" co-vibration conditions were significantly (v-test, $P<0.0001$) close to the expected directions. In addition, the amplitude of the mean postural response increased, so that the length of the mean experimental vector did not differ significantly (*t*-test, $P>0.05$) from that of the theoretical vector (Fig. 4B).

In short, the results obtained on the whole population show the following:

1. Whether applied at the neck or ankle level, vibratory stimulation induces whole body displacements, whose direction depends specifically on the muscle group stimulated.
2. These postural responses occur in opposite directions, depending on whether the neck or ankle muscle groups are stimulated; when vibration was applied at the neck level, the postural responses were oriented contralaterally to the vibrated muscle site, and conversely when vibration was applied at the ankle level.
3. In addition, except for co-stimulation of the ankle antagonist muscles, the CoP shifts induced when vibration was applied simultaneously to two muscle groups (adjacent or antagonist) at the same body level were similar in terms of their amplitude and direction to the sum of the two separate vibration-induced effects.

4. This vector-addition law was also valid in the case of the “concordantly” and “discordantly” acting patterns of co-vibration applied simultaneously at the two body levels.

Discussion and conclusion

The role of ankle-versus neck-muscle proprioceptive messages for postural control

The finding that vibration applied to a specific group of muscles can induce distinct postural reactions in a specific direction agrees with previous studies (Eklund 1972; Gregoric et al. 1978; Gurfinkel et al. 1977; Lund 1980; Roll and Roll 1988; Roll et al. 1989b; Smetanin et al. 1993). It suggests that muscle proprioceptive inputs originating from body parts as far apart as the ankle and neck can equally contribute to postural control. However, why vibration applied to the muscles on the same body side gives rise to body tilts in opposite directions remains unclear.

For the ankle muscles, the direction of the postural responses was counter to the direction of the muscle lengthening simulated by applying vibration (Roll et al. 1989a). Indeed, when the nervous system receives a muscle-spindle message indicating that the vibrated muscle has lengthened and that the body’s balance is liable to be upset, a postural response tending to restore the initial body position is triggered. Although this regulatory response is actually unnecessary, since the body has not really moved, it causes the body to move in the opposite direction.

For the neck muscles, on the contrary, vibration gave rise to body tilts in the same direction as the lengthening simulated in the vibrated muscle. One explanation is that this response results from a combined processing of both neck-muscle and vestibular-proprioceptive information. For example, in the case of dorsal neck-muscle vibration, a proprioceptive message indicates that the head is inclined forward with respect to the trunk, while the vestibular signal indicates that the head remains straight. A possible interpretation would be that the trunk is swaying backward with respect to the head (as if the subject’s feet were sliding forward). As a consequence, the postural sway directed forward in response to the splenii vibration will be a compensatory response returning the body upright (Lekhel et al. 1996). This interpretation is in agreement with various studies showing that the central nervous system is able to integrate the vestibular and neck proprioceptive information to subserve postural control (Gurfinkel et al. 1995; Hlavacka et al. 1985; Lund and Broberg 1983). However, when the body is mechanically restrained, the same stimulation of the dorsal neck muscle evokes either a head (Smetanin et al. 1993) or whole body (Roll et al. 1994) illusory displacement, which is always directed forward; it never induces a body-sway illusion beneath the fixed head with the neck as an axis of rotation. Moreover, an additional input coming from the foot soles also has to be taken into account by the central nervous system. Under our experimental context, this tactile input indicates that the body is unmoving, as the vestibular input indicates that the head remains stable.

Finally, a more functional interpretation may be put forward. It is based on the fact that vibration applied to muscle groups at the eye (Roll and Roll 1987; Roll et al. 1991), neck (Gurfinkel et al. 1988; Lekhel et al. 1996; Lund 1980), and upper trunk (Gregoric et al. 1978; Smetanin et al. 1993) levels gives rise to body tilts in the same direction as the lengthening of the vibrated muscle. This could be taken to mean that the muscle stretching during eye-, head-, or upper-trunk-orienting movements in a given direction might elicit whole-body oriented postural activities in the same direction. Data from Roll and Roll (1987, 1988) showed that backward and forward body tilts occurred after inferior and superior eye-muscle vibration, respectively. In the case of a sustained version of the eyes, the stretching of the lateral rectus of one eye and medial rectus of the other eye resulted in an increase in the muscle tone in the leg ipsilateral to the version (Gantchev et al. 1985).

In addition, concerning the role of the neck muscle, Fukuda demonstrated that the orientation of the subject’s whole-body displacement during on-the-spot stepping depends strictly on head position (straight ahead, left, or right) (Fukuda 1959; Ushio et al. 1976). Likewise, the whole-body tilts in response to either neck vibration (Lekehl et al. 1996; Smetanin et al. 1993) or galvanic vestibular stimulation (Gurfinkel et al. 1995; Hlavacka and Njiokiktjien 1985; Lund and Broberg 1983) were spatially re-oriented toward the direction in which the subject’s head was turned. Taken together, these results suggest that the muscle proprioceptive information arising from the muscles at the upper-body level mainly participate in the postural-orientation processes involved in goal-directed behavior.

Multiple proprioceptive information serves to regulate and orient a single posture

The integration of multiple proprioceptive information arising from a single body level

Whenever we applied co-vibration at either the neck or ankle level, the postural response observed was, except for one experimental condition, the sum of the responses obtained when the vibration was applied separately to each of the muscle groups in question. When co-stimulation was applied to two adjacent muscles, each of which triggered orthogonal postural reactions when vibrated separately, the direction of the jointly elicited postural sways was an intermediate one. More specifically, when the mean postural tilts in each experimental condition were expressed as vectors giving both the direction and the amplitude of the effects of applying co-stimulation to two adjacent muscles, these vectors did not differ significantly from the theoretical result consisting of the sum of the two mean vectors obtained when each of the muscles in question was vibrated separately.

Likewise, co-stimulating two antagonist muscle groups that elicited postural reactions in opposite directions when vibrated separately resulted in a response with a very small amplitude. On average, the amplitude of the postural reactions was very much in line with that expected when antagonist muscles at the cervical level were co-stimulated; this was not the case, however, at the ankle level, where the theoretical value was greater than that obtained experimentally in response to the co-stimulation. Although the mean postural shifts elicited by vibrating the tibialis anterior and soleus muscles separately were in opposite directions, the sum of their amplitudes gave a relatively high value because their isolated amplitudes differed considerably among subjects. This discrepancy between the theoretical and experimental results might be attributable to ankle biomechanical constraints, which make it possible to perform greater-amplitude forward than backward body movements (Lestienne et al. 1977). In fact, Eklund and Lofstedt (1970) have shown that only 37% of the base of support provided by the Feet is posterior to the center of rotation; consequently, the maximum backward tilt is smaller than the forward one. During the co-vibration of the two antagonist muscle groups, however, such biomechanical constraints no longer occurred, since the postural responses did not go beyond the limits of the body equilibrium.

On the whole, the above data suggest that all the proprioceptive information arising from two or more muscles at a given body level concomitantly undergoes sensorimotor processing, in keeping with vector-addition laws. This integrative mechanism, which permanently processes proprioceptive messages arising from a whole set of muscles, is somewhat reminiscent of that at the perceptual level, coding the direction and the velocity of ongoing vibration-induced illusory movements on the basis of the vector sum of the information arising from all the muscles involved (Roll and Gilhodes 1995). In addition, Roll et al. (1991) also reported that the proprioceptive inputs originating from antagonist muscle groups at the neck level might be summed to contribute to specifying the gaze direction necessary for spatial localization task. The existence of analogies of this kind indicates that the mechanisms underlying the perceptual integration of proprioceptive information and those whereby this information is transformed for sensorimotor purposes, such as postural orientation and regulation, might obey laws that have much in common.

The integration of multiple proprioceptive information arising from two body levels

The results show that the postural responses evoked when neck and ankle muscles are stimulated jointly may be equal to the sum of the effects induced by applying vibratory stimulation to muscles at each of these body levels separately. The proprioceptive information arising simultaneously from the cervical and ankle musculatures, therefore, seems to be integrated on the basis of a vector-addition mode. This idea is in keeping with data by Wolsley et al. (1996), who reported that the direction of visually induced body sways was modified with respect to the orientation of the gaze. In this case, the body sways were re-directed toward the direction in which the eyes and head were turned together. The same coupling of extraocular, neck, and ankle proprioceptive information for postural control was also described by Roll and Roll (1988), supporting the previous hypothesis that there may exist a functional proprioceptive chain, whose links may be functionally interdependent.

On the other hand, it has been proposed elsewhere that this vectorial principle might also be applied to the integration of multimodal sensory information for postural control (Hlavacka et al. 1995). They put forward the idea that the central nervous system may ensure that the erect posture is maintained by making use of an internal body vertical reference value, which is the vector sum of various reference vertical values, each of which is specified on the basis of muscular, vestibular, and visual information. The results of other studies in which the contributions of the vestibular and proprioceptive sensory inputs were jointly tested (Gurfinkel et al. 1988; Karnath et al. 1994) further support the idea that information arising from various sensory sources may undergo a co-processing of the integrative type for postural purposes.

Despite these arguments favoring the hypothesis of a high-order processing of various proprioceptive cues, one cannot rule out that this integration could be based on a linear summation of short or long-loop reflexes, mainly because the muscle responses are known to occur between 100 and 200 ms, depending on the stimulated site and recorded muscles. However, neurophysiological data from Burke and Eklund (1977) and Hagbarth (1973) have also suggested that stretch reflexes alone failed to explain the vibration-induced body sways. Therefore, which of these apparently opposing mechanisms is predominant remains to be demonstrated.

Finally, the present results suggest that muscle inputs may be preferentially involved in specific postural functions, depending on the body-level. Nevertheless, they also show that multiple proprioceptive information is integrated by the central nervous system in order to permanently orient the body appropriatly while keeping balance.

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