

John J. Jeka · James R. Lackner

Fingertip contact influences human postural control

Received: 10 September 1993 / Accepted: 4 April 1994

Abstract Touch and pressure stimulation of the body surface can strongly influence apparent body orientation, as well as the maintenance of upright posture during quiet stance. In the present study, we investigated the relationship between postural sway and contact forces at the fingertip while subjects touched a rigid metal bar. Subjects were tested in the tandem Romberg stance with eyes open or closed under three conditions of fingertip contact: no contact, touch contact (<0.98 N of force), and force contact (as much force as desired). Touch contact was as effective as force contact or sight of the surroundings in reducing postural sway when compared to the no contact, eyes closed condition. Body sway and fingertip forces were essentially in phase with force contact, suggesting that fingertip contact forces are physically counteracting body sway. Time delays between body sway and fingertip forces were much larger with light touch contact, suggesting that the fingertip is providing information that allows anticipatory innervation of musculature to reduce body sway. The results are related to observations on precision grip as well as the somatosensory, proprioceptive, and motor mechanisms involved in the reduction of body sway.

Key words Fingertip · Posture control
Spatial orientation · Touch · Human

Introduction

The primary sensory inputs to postural control are visual, proprioceptive, and vestibular (Nashner 1981). Less well studied is the influence of somatosensation on postural equilibrium. In combination with proprioceptive inputs from the legs and ankles, somatosensory stimula-

tion from contact of the feet with the support surface has been shown to play an important role in maintaining upright stance (Diener et al. 1984). Moreover, a growing body of evidence suggests that touch and pressure cues from *any* part of the body in contact with a stable external surface may have a profound influence on apparent body orientation (Lackner 1981, 1992). This implicates a larger role for touch cues in the control of posture than presently conceived.

The influence of touch inputs has been illuminated particularly by studies of body orientation illusions. Several studies have shown that somatosensory stimulation of the hands or feet can elicit illusions of body motion in blindfolded subjects (Brandt et al. 1977; Lackner and DiZio 1984), even to the point of inducing nystagmus compensatory for the direction of apparent body motion. Moreover, Gurfinkel and Levik (1994) have shown that the cervico-ocular illusion, the sensation of head rotation in space when the trunk is rotated at slow speeds with respect to the stationary head, is suppressed by grasping a rigid ground-based handle during trunk rotation. The tactile and proprioceptive cues from the arm provide veridical information about trunk orientation to a stable external referent, overriding the body-centered reference. Interestingly, when the handle was compliant rather than rigid, suppression of the cervico-ocular illusion was not reported.

Tendon vibration studies have also revealed that contact with an external surface can modify proprioceptive inputs to the perception of body orientation. If the achilles tendons of a standing subject are vibrated while he or she is restrained in position and blindfolded, illusory forward body tilting is reported, centered around the ankles. However, if the subject is provided with contact cues through a bite plate, the pivot point of tilt often changes from ankles to head. Experienced tilt occurs despite no change in stimulation to the otolith receptors, which are often considered the primary influence on the preception of postural upright (Benson 1982; Howard 1986). Furthermore, the patterns of body motion experienced during z-axis recumbent rotation of

J. J. Jeka (✉) · J. R. Lackner
Ashton Graybiel Spatial Orientation Laboratory,
Brandeis University, Waltham, MA 02254, USA,
e-mail: jeka@binah.cc.brandeis.edu

the body ('barbecue spit rotation'), which have traditionally been related to vestibular stimulation (Correia and Guedry 1966) turn out to be attributable to touch and pressure stimulation of the body surface which is covarying with the vestibular activity (Lackner and Graybiel 1978a, b).

In view of such findings, touch cues may also be expected to influence the maintenance of upright posture during quiet stance or locomotion. Intuitively, we conceive of contact with a stable surface, such as leaning against a wall with the hand and arm, as providing postural stabilization through passive physical reaction forces that balance those imposed by movement of the body. However, touch contact does not have to be physically supportive to influence balance. Marsden et al. (1981) showed that perturbations as small as 7.5 g applied to the left thumb of a standing subject resulted in compensatory postural responses similar to those observed with loads of 300 g or more. More recently, Holden et al. (1987, 1994) have found that contact of only a fingertip with a stationary surface can attenuate postural sway, even when contact forces may not be large enough to provide significant physical support.

In the present experiment we investigated whether the reduction of postural sway conferred by light touch of the index finger is due to the sensory information about body sway it provides. Our approach was to compare the temporal relationship between body sway and contact forces at the fingertip for force levels that are: (1) large enough to provide some actual physical stabilization of the body ($\approx 400\text{--}500$ g); and (2) too small to provide physical support (< 100 g). When fingertip contact is providing physical support, we expect force level to increase and decrease with body sway towards and away from the contact surface, respectively. When fingertip contact force is too small to provide physical support but can possibly provide sensory cues about body sway, we expect body sway to lag contact force changes at the fingertip, because the role of the sensory cues would be to allow anticipatory innervations of the leg musculature to reduce sway. We were also interested to see how contact cues from the fingertip influence the spectral properties of postural sway. Somatosensory and proprioceptive input from the feet and ankles (Diener et al. 1984), as well as vision (Dichgans and Brandt 1973; Mauritz et al. 1979), are known to influence posture primarily at sway frequencies below 1 Hz. We tested subjects with eyes open and with eyes closed, with and without fingertip contact cues, to see whether touch cues from the fingertip would influence postural sway in the same frequency range.

Materials and methods

Apparatus

Figure 1 depicts a subject in the tandem Romberg stance (heel-to-toe) on a force platform while touching the device used to measure the forces applied by the right index fingertip. The force platform

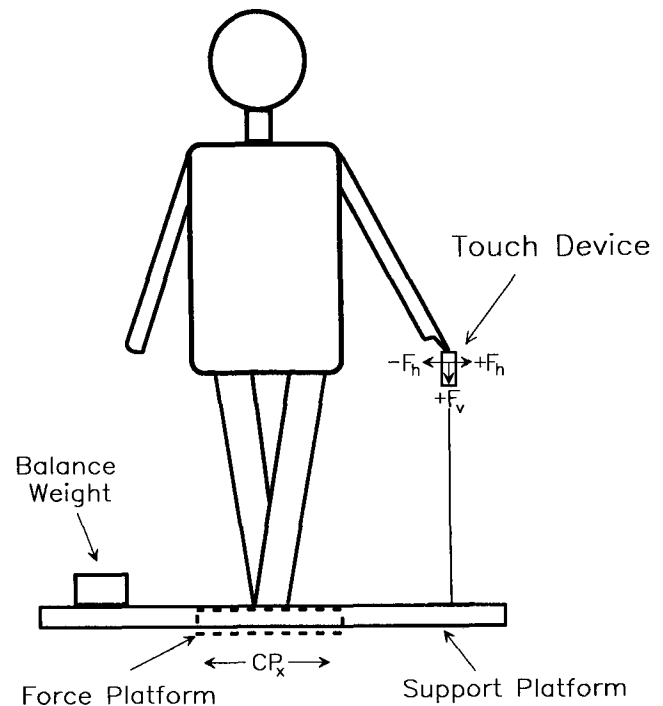


Fig. 1 Subject depicted in tandem Romberg posture on the force platform in the touch (VT, DT) and force (VF, DF) contact conditions with the right index fingertip on the touch bar. In the no contact (V, D) conditions, the subject's arms hung passively by his or her side

(Kistler Model 9261A) measured the medial-lateral (CP_x) and anterior-posterior (CP_y) center of foot pressure coordinates from the force components (F_x , F_y and F_z) of the active forces applied to its surface registered by piezo-electric crystals in each of the four corners of the platform.

The touch device consisted of a horizontal metal bar ($46\text{ cm} \times 1\text{ cm} \times 2\text{ cm}$) attached to a metal stand, parallel with the subject's sagittal plane. The stand rested on a rigid wooden platform ($155\text{ cm} \times 70\text{ cm}$) that overlaid the force plate. The wooden platform extended beyond the lateral edges of the force plate; the touch device apparatus rested on the right side and was balanced by a comparable weight on the left side. This arrangement ensured that the computed center of pressure reflected movements and acceleration of the subject's center of gravity, and would not be affected directly by forces applied at the fingertip. The horizontal bar could be adjusted in height and position to allow individual subjects to assume a comfortable arm position while touching the contact surface with their index finger. The subject placed his or her right index finger on the middle of the bar which was marked with a small piece of white tape. Two dual element, temperature-compensated strain gauges (Kulite Semiconductor, Type M(12) DGP-350-500) mounted on the metal bar transduced the horizontal (F_h) and vertical (F_v) forces applied by the finger. The strain gauge signals were amplified and calibrated in units of force (newtons) and a comparator could trigger an auditory tone when an adjustable threshold force was reached. Five data channels (force platform: CP_x , CP_y and F_z , touch device: F_h and F_v) were digitized in real time at 64 Hz using a personal computer with a data acquisition board (Data Translation DT-2800).

Subjects

Five individuals participated, one woman and four men ranging in age from 20 to 50 years. The subjects were healthy and physical-

ly active with no known musculoskeletal injuries or neurological disorders that might affect their ability to maintain balance.

Procedure

The subject stood with right foot directly behind left along the center of the anterior-posterior axis of the force platform. Adhesive tape was used to mark the position of the feet on the platform so that the same foot position could be repeated on each trial. The touch bar was adjusted to a comfortable height and distance for the right fingertip.

The experimental trials included two visual conditions (vision, eyes open, and dark, eyes closed) and three fingertip contact conditions (no contact, during which the subject's arms hung passively, touch contact, in which the subject was limited to 0.98 N of applied horizontal or vertical force on the touch apparatus, and force contact, during which the alarm was turned off and subjects could apply as much force as desired). The six experimental conditions are identified as follows: V = vision – no contact, VT = vision – touch contact, VF = vision – force contact, D = dark – no contact, DT = dark – touch contact and DF = dark – force contact.

Subjects began each trial by looking straight ahead at a fixation target on a wall 2 m away covered with a black cloth. The subjects peripheral visual field beyond 30° provided a rich, complex visual environment with horizontal and vertical cues. Before each trial, subjects were told to look straight ahead and to take as much time as desired to assume a comfortable stance with their fingertip on or off the touch bar and with eyes open or closed, depending upon the condition. Their instructions were to maintain the tandem stance as comfortably as possible for the entire trial, to sway as little as possible, and to keep the fingertip on the same spot on the touch bar during the touch and force contact trials. Once they felt ready, subjects said 'go' and the experimenter initiated data acquisition. Practice trials were given for each condition before the experiment began. If a subject was unsuccessful in a particular practice trial (e.g., lost balance or triggered the touch alarm more than once), then that trial was repeated until performed correctly. Every subject successfully completed each practice condition within two attempts.

The experimental trials were run in four blocks of six trials (one of each condition per block) for a total of 24 trials. Conditions were randomized within a block. Trial duration was 24 s. If a subject was unable to complete a particular trial (e.g., lost balance), it was repeated immediately. After each trial, the subject stepped off the platform and sat comfortably for at least 1 min. The experiment lasted approximately 1 h.

Analysis

To minimize contamination from possible anticipation effects associated with the beginning and end of a trial, the first 4 s and the last 4 s of data were excluded from consideration, leaving 16 s of data for each trial. Cross-correlations between the fingertip contact forces (F_h and F_v) and center of pressure sway (CP_x and CP_y) sway were calculated to determine which components were most strongly related in time. Correlations were performed at each of 100 steps (15.625 ms/step) in both the forward and backward directions to determine if correlations were strongest at times other than $t=0$ (i.e., in phase). Because correlations do not have a normal distribution, correlations were first transformed to the Fisher's z for statistical analysis (Senders 1958). Planned comparison t -tests demonstrated that the CP_y - F_h and CP_y - F_v correlation pairs were never significantly different from zero. Thus, since CP_y was not correlated to the touch bar forces, further analyses focused on measures to characterize the influence of fingertip contact forces on only CP_x sway.

CP_x sway amplitude within a trial was determined by subtracting the average position of CP_x from each data point. CP_x mean sway amplitude (MSA) was equal to the average variation around the mean position of CP_x . Mean sway velocity (MSV) was also

calculated by differentiating CP_x sway amplitude and calculating the average velocity within a trial. Mean horizontal and vertical forces applied by the fingertip were calculated for the touch and force contact conditions. A power spectral density analysis was performed to determine the component frequencies of CP_x sway. Analyses of the power spectra were used to identify the bandwidth between 0 and 4.0 Hz in which over 95% of the power was concentrated. CP_x sway mean power frequency ($MPF = \sum p f d f / \sum p d f$) and mean total power ($MTP = \sum p d f$), where p equals the power at frequency f , were calculated within this bandwidth.

A $2 \times 3 \times 4$ repeated-measures MANOVA was performed to evaluate the influence of vision (V,D), contact (none, T, F) and trial (1–4) factors on CP_x sway for measures (MSA, MSV, MPF & MTP). Because contact forces were zero in the no contact condition, a separate $2 \times 2 \times 4$ MANOVA was run for measures involving contact forces (mean absolute F_h and F_v , CP_x - F_h correlation and time lag, CP_x - F_v correlation and time lag), with only the t and F levels of the Contact factor. Since our overall analysis involved two separate MANOVAs, which may inflate Type I error, our level of significance was adjusted with a Bonferroni correction for multiple tests (Kirk 1982). Therefore, a MANOVA effect was not considered significant at the 0.05 level unless its tabled F -value had a $P < 0.025$. Follow-up univariate ANOVAs were also adjusted using the Bonferroni correction, resulting in a required significance level of 0.005 for each ANOVA.

The effect of trial order was not significant in both the CP_x sway and touch MANOVAs ($P > 0.1$), therefore the data were averaged across trials for each subject. The results of the CP_x sway MANOVA showed significant effects for the vision and contact factors and the vision \times contact interaction ($P < 0.001$). The contact force MANOVA showed significance only for the contact factor ($P < 0.001$). The details of the univariate ANOVAs and pairwise comparisons are discussed in the results section.

Results

Mean sway amplitude

Mean CP_x sway amplitude was highest in the dark-no touch (D) condition and was significantly reduced in all other conditions. Figure 2a shows the CP_x sway of subject 1 in a dark-no contact (D) condition overlaid upon a dark-touch (DT) condition, illustrating the reduction in medial-lateral sway due to the addition of touch contact. Figure 2b displays the mean CP_x sway amplitude in each condition collapsed across subjects. A statistical analysis revealed a significant vision \times contact interaction effect for CP_x sway ($P < 0.001$). Further comparisons of CP_x sway amplitude revealed three influences of visual and contact information:

(1) CP_x mean sway amplitude was significantly greater in no contact than touch contact conditions ($D > DT$ and DF , $V > VT$ and VF , $P < 0.01$), indicating that touch and force contact effectively reduced CP_x mean sway amplitude, with or without vision present.

(2) CP_x mean sway amplitude in the dark touch condition was significantly lower than in the vision no contact condition ($V > DT$, $P < 0.01$), indicating that touch contact was more effective than vision in reducing postural sway in the tandem Romberg stance.

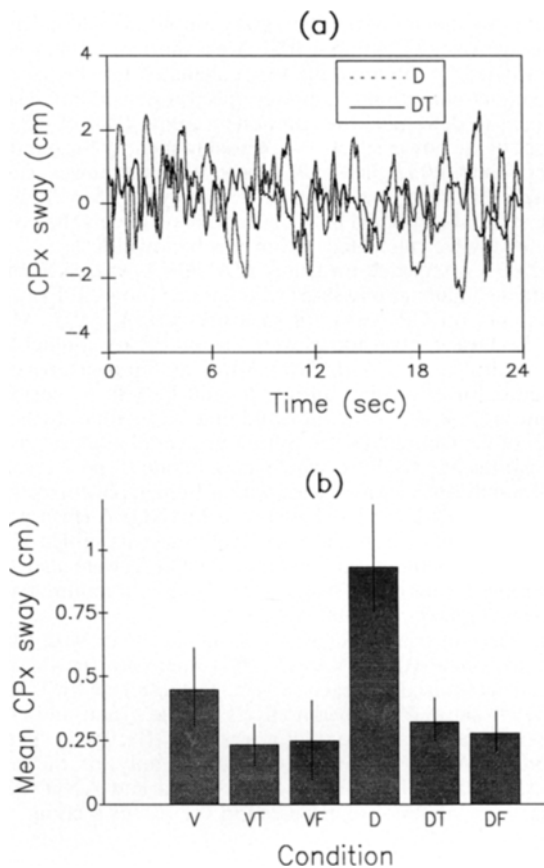


Fig. 2 **a** Overlaid time series of CP_x sway from dark – no contact (dotted line) and dark – touch contact (solid line) conditions illustrating the reduction in CP sway amplitudes due to fingertip touch contact. **b** Mean CP_x sway amplitude (MSA) collapsed across subjects for each experimental condition. MSA was highest in the no contact – dark (D) condition and lowest with any form of fingertip contact. Error bars are SDs in this and subsequent figures

(3) CP_x mean sway amplitude was greater with eyes closed than eyes open in the no contact ($D > V$, $P < 0.001$) and touch contact conditions ($DT > VT$, $P < 0.05$), but not different with force contact ($DF = VF$). Force contact mechanically stabilizes postural sway to such an extent that vision can provide no additional stabilization.

Fingertip contact forces

The mean absolute vertical and horizontal forces at the fingertip are shown in Fig. 3 for the conditions involving fingertip contact. Increases in both horizontal and vertical forces were observed from conditions using touch contact (VT and DT) to those using force contact (VF and DF).

Differences in mean contact force levels were significant only for contact with both the horizontal and vertical forces ($P < 0.0001$). There were no significant differences due to vision ($P > 0.05$).

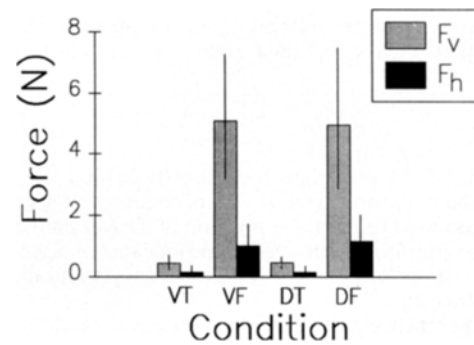


Fig. 3 Mean horizontal and vertical fingertip forces collapsed across subjects in each experimental condition involving fingertip contact. Contact forces were approximately ten times greater with force contact than touch contact

CP_x-F_h and CP_x-F_v correlations

Figure 4a, b shows overlaid time series of CP_x sway and F_h in the VF and VT conditions with their respective correlations and time lags. The correlation between CP_x sway and F_h is higher in condition VF (Fig. 4a) than condition VT (Fig. 4b). Moreover, the time lag at which the maximum correlation occurs is much longer in VT (lag ≈ 296 ms) than VF (lag ≈ 31 ms). This means that changes in CP_x sway and F_h occur at approximately the same time with force contact (VF), while changes in CP_x sway occur approximately 300 ms after changes in F_h with touch contact (VT).

The differences in correlation and timing between CP_x sway and contact forces as shown in Fig. 4 for individual trials were also reflected in mean values. Mean CP_x-F_h & CP_x-F_v correlations, collapsed across trials and subjects, are shown in Fig. 5a and Fig. 5b, respectively. Statistical analysis revealed a significant main effect for contact for both CP_x-F_h and CP_x-F_v correlations ($P < 0.0001$), highlighting the increase in mean correlations from the touch to the force contact conditions.

The average time lags at which the maximum correlations were found in each condition are also shown in Fig. 5a, b. CP_x-F_h and CP_x-F_v time lags increased on average by over 200 ms from the force (DF and VF) to the touch (DT and VT) conditions. These increases were significant ($P < 0.001$). In every case, the time lags were positive, meaning that changes in contact forces at the fingertip were ahead of changes in CP_x sway.

Power spectra

The CP_x mean power frequency (MPF) of each condition is shown in Fig. 6a. MPF of CP_x sway hovered around 0.5–0.6 Hz and showed no statistical differences across conditions ($P > 0.1$).

CP_x sway mean total power, shown in Fig. 6b, was clearly influenced by vision and fingertip contact forces. It was highest in the dark (D) condition, and decreased

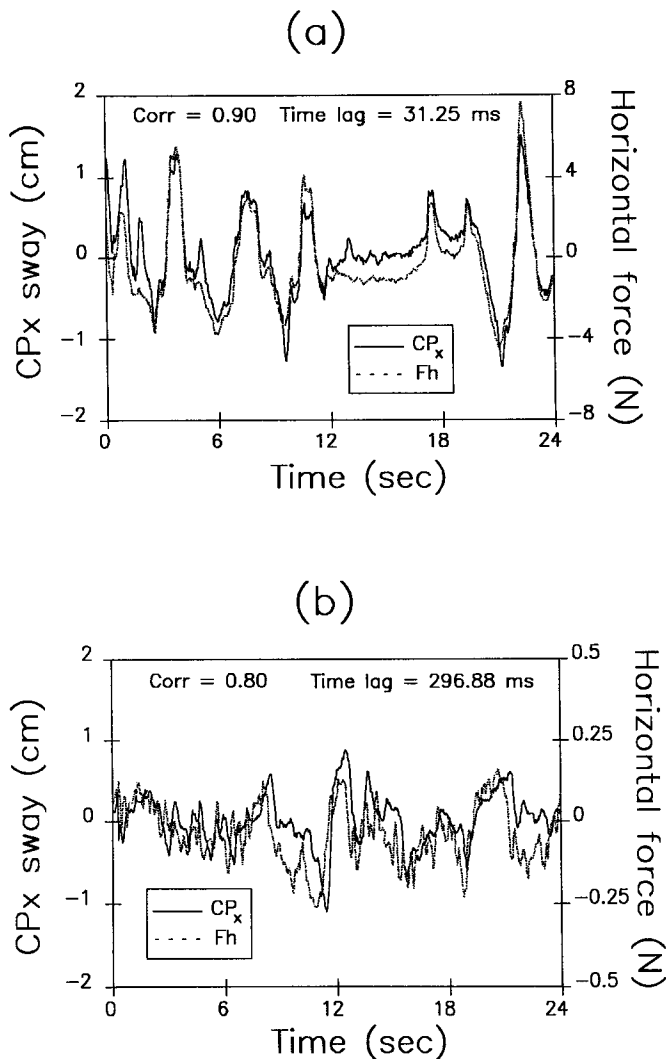


Fig. 4 Overlaid time series of CP_x sway (solid line) and horizontal fingertip force (dotted line) in (a) vision-force contact (VF) and (b) vision-touch contact (VT) conditions. Individual correlations and time delays for each trial are shown. Note different scales of fingertip force are used on right y-axes of (a) and (b)

when vision or fingertip was added, as shown by a significant vision \times contact interaction effect ($P < 0.0001$). Together, the MPF and MTP results clearly show that touch inputs stabilize postural sway similar to vision.

Sway velocity

CP_x mean sway amplitude was significantly larger in the (D)ark and (V)ision conditions, but CP_x mean power frequency was equivalent across all conditions, implying that sway velocity must have increased in the D and V conditions. Figure 7 confirms that CP_x sway velocity increased in each condition in which mean CP_x sway amplitude was also greater (compare with Fig. 2b). A statistical analysis revealed a significant vision \times contact interaction effect ($P < 0.0001$), primarily due to the increase in CP_x sway velocity in the (D)ark condition.

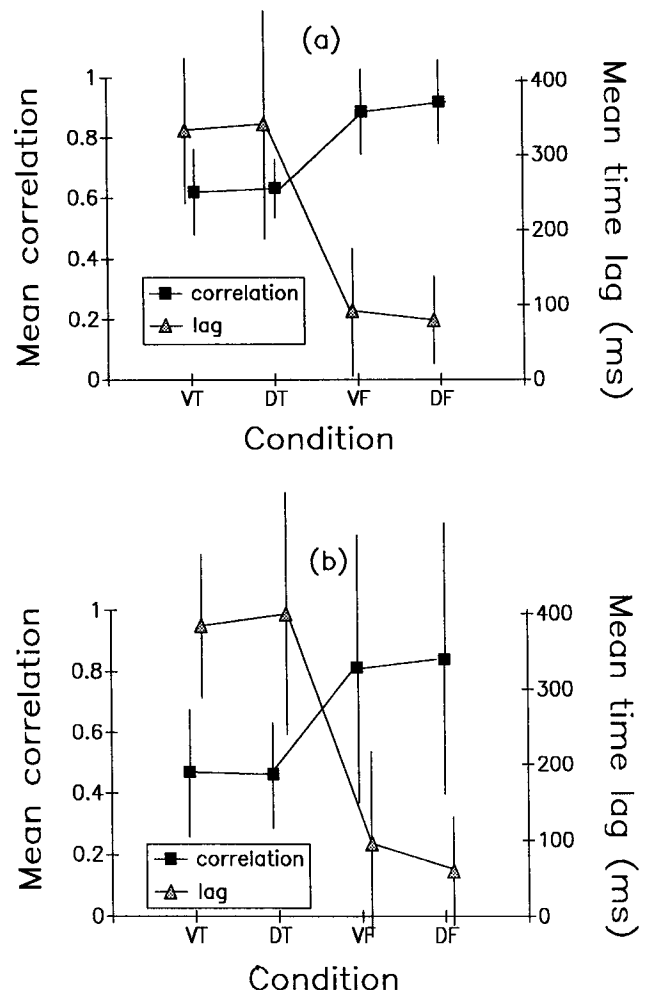


Fig. 5 Mean correlations and time delays for (a) CP_x - F_h (b) CP_x - F_v . Mean correlations were higher with force contact than touch contact. Time lags increased from ≈ 80 ms with force contact to ≈ 300 ms with touch contact. Positive time delay means first variable of correlation pair lags the second variable in time

Discussion

Contact of the index finger with a stationary bar attenuated postural sway in the tandem Romberg stance when subjects stood without sight of their surroundings¹. The reduction in amplitude (Fig. 2b) and spectral power (Fig. 6b) of body sway provided by fingertip contact was even greater than that contributed by allowing

¹ We recognize that center of pressure movement is not equivalent to center of body mass movement. Center of pressure movements tend to be larger and of higher frequency than center of mass movements (cf. Winter et al. 1990). To evaluate this relationship in the present situation a video system was set up to track a single LED located at a subject's navel as a measure of center of mass movements. In a retest of the experiment with two subjects from the original group, we found: (1) body sway to change proportionally to CP sway in each condition; and (2) correlations between CP_x sway and medial-lateral body sway to average 0.89 with a 2.3 ms time lag across all conditions. Thus, we may safely assume that, in the present study, all statements concerning CP sway apply as well to movements of the center mass

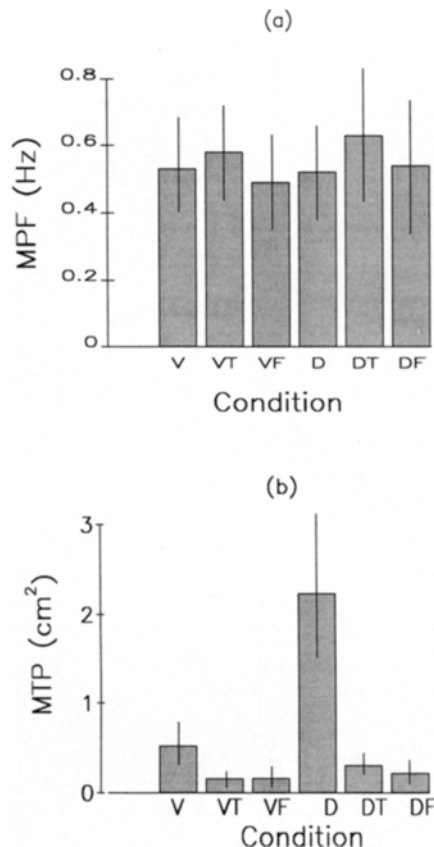


Fig. 6 (a) Mean power frequency (*MPF*) and (b) Mean total power (*MTP*) collapsed across subjects for CP_x sway in each experimental condition. *MPF* changed very little across conditions. The primary influence of vision and fingertip contact was on *MTP*

sight of the surroundings. This was the case even though the force levels at the fingertip in the touch contact conditions were totally inadequate in providing significant mechanical stabilization of the body. In the conditions involving force contact of the index finger, the fingertip forces generated were almost fifteen-fold greater and adequate in providing significant mechanical stabilization of the body, albeit not to the level actually observed.

Changes in contact force at the fingertip were highly correlated to body sway; however, the temporal relationship between medial-lateral sway and fingertip contact force differed for the touch and force contact conditions, as we expected (see Fig. 5a). With force contact, body sway lagged the finger force signal by approximately 80 ms. In the touch contact conditions, there was a considerably greater time lag between medial-lateral sway and force at the fingertip, about 300 ms. The nearly in-phase relationship between body sway and fingertip contact forces in the force contact conditions (VF and DF) implies that fingertip contact forces are used to offset physically movements of the body's center of mass during force contact conditions. However, in the light touch, contact conditions, contact cues provide information about the *position* of the body. An increase in the horizontal fingertip force indicates body sway to the

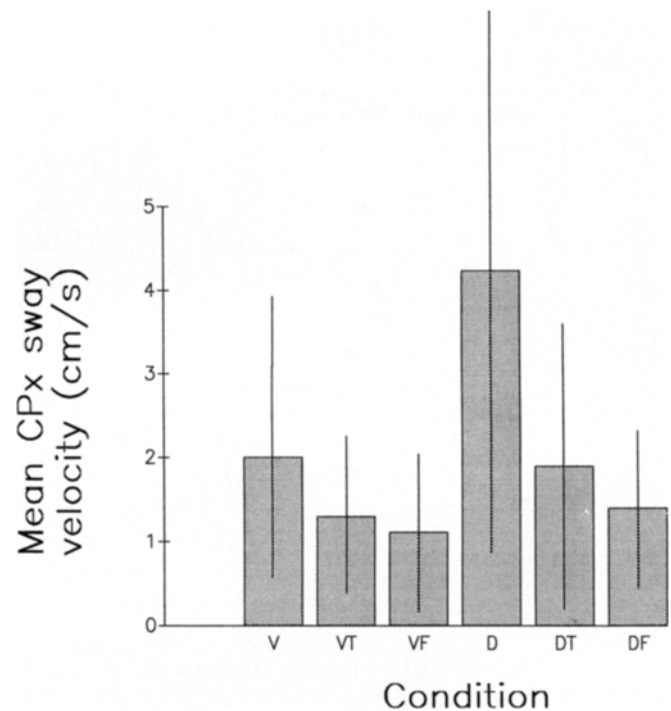


Fig. 7 Mean CP_x sway velocity (MSV) collapsed across subjects for each condition. MSV followed the same pattern of results as MSA (see Fig. 2b)

right, while a decrease in horizontal fingertip force indicates leftward sway. Some subjects were partly aware of this relationship between fingertip force and body position and later reported consciously 'letting up' on their finger as they swayed to the right, in order not to set off the alarm. This partially explains why fingertip forces in touch contact trials consistently led body sway. Because fingertip forces were not allowed to be large enough to balance center of mass movements, postural muscles had to be activated to counteract sway. Two to three hundred milliseconds is a reasonable time for reversing the direction of sway from a lateral to a medial direction. Nashner (1976) has found, for example, that EMG activity occurs within 100 ms in response to perturbations of a standing subject's base of support, but that actual compensatory changes in sway can take 300 ms and longer to appear. These values correspond to those observed in our touch contact conditions: thus, EMG activity in postural musculature related to fingertip cues may be occurring within 100 ms, while the time delays associated with overcoming the inertial forces of body sway may be closer to 300 ms. We are currently evaluating this possibility.

To enhance postural stability using contact cues from the finger, it is necessary to monitor accurately the overall configuration of the arm in relation to the torso and to register motion, displacement, and force level at the fingertip. Changes in arm-torso configuration and in the relation of the finger to the touch bar in the absence of voluntary arm and hand movements are due to move-

ments of the subject's torso and therefore signal body sway. Similarly, changing stimulation at the fingertip without changes in arm joint angles also means the body is swaying. Subjects must be able to interpret either situation correctly in order to make appropriate postural corrections.

A variety of physiological mechanisms are involved in postural stabilization by fingertip contact. Phillips (1985) has referred to the glabrous skin of the fingertip as the 'somesthetic macula', analogous to the fovea of the retina. He highlights a number of parallels between control of the eyes and of the fingers in terms of acquisition of targets and maintenance of 'fixation'. As he points out, voluntary movements of the hand are supplemented by reflexes that maintain the hand in contact with objects of interest. Such an emphasis on 'active touch' (see also Gordon 1978) is crucial in understanding the present experimental observations.

Knowledge of ongoing arm configuration is dependent on interrelating muscle afferent and other proprioceptive activity to motor commands (Burgess et al. 1982; Matthews 1981, 1988). Area 3a of primary somatosensory cortex receives muscle spindle signals from the arm and hand, and projects directly to topographically related parts of area 4, the primary motor cortex, as well as to parietal cortex. In area 5 of parietal cortex, some neurons are 'kinesthetically truthful' and signal the direction of joint displacement whether achieved actively or passively (Phillips 1985). The patterns of connectivity of area 3a and area 4 also provide the anatomical basis for Phillips concept of an automatic, transcortical loop by which compensatory responses involving suprasegmental, long loop responses can be initiated with 50 ms of a perturbation.

Interestingly, Marsden et al. (1981) have demonstrated that compensatory reactions in response to a perturbation can be at a 'distance', if the perturbation disturbs an individual's upright stance. For example, compensatory activation of leg muscles will occur in response to a perturbation of the forearm in a standing subject. The key point is that leg muscle activity leads the actual displacement of the body, so that it is not a reflexive response to stretch of the leg muscles but an anticipatory innervation. These observations are fully consonant with the patterns observed in our light touch conditions.

The receptors of the index fingerpad are quite well suited to providing information about the position and configuration of the finger in relation to the touch bar in our experiment. For example, cutaneous receptors are known to discharge in relation to joint angle (Hullinger et al. 1979; Knibestöl 1975) so that finger joint movement can – in relation to other information about arm position – provide information about body sway. Slowly adapting (SA) cutaneous receptors, which are primarily responsible for tactual form and roughness perception through the distribution of forces across the skin surface (Johnson and Hsiao, 1992), may also provide information about body sway with light touch contact through skin surface deformation (i.e., vertical or nor-

mal forces) or through 'skin stretch' (i.e., horizontal or shear forces) that is quite accurate and sensitive. For example, Srinivasan et al. (1990) have measured detection thresholds for movement of a polished glass plate across the fingerpads. At levels of contact force equivalent to those in our light touch contact conditions (≈ 20 g), when the plate was moved only enough to stretch the skin, its direction of motion was identified accurately more than 90% of the time. Subjects in our touch contact conditions thus can use the direction of index finger skin stretch and skin surface deformation to identify the direction of body sway movements.

Further support for this interpretation can be found in 'precision grip' studies (Johansson 1991) in which the activity of single afferent fibers from cutaneous receptors in the fingertip is recorded while objects are lifted with the thumb and index finger. Maximal afferent activity is observed at approximately 30–50 g of load force (Westling and Johansson 1987). In the present experiment, all subjects spontaneously adopted equivalent levels of contact in the light touch contact conditions (≈ 40 g) even though they were allowed up to 100 g of force. This means that our subjects home in on a contact force range where receptor sensitivity is greatest and provides the highest resolution of directional change.

Finally, the present paradigm with touch contact of the index finger may be envisioned as the entire body participating in a precision grip with the contact force on the fingertip being controlled. The index finger and arm form one segment of a pincer, the legs and torso, the other. The leg muscles are activated in a fashion such as to keep the force level at the index finger around 40 g and thereby reduce postural sway. That parts of the body not normally involved in precision grip could function in such a fashion should not be considered surprising. In postural tasks involving lifting or grasping, remote adjustments of body musculature shift the center of mass in an anticipatory fashion for the expected consequences of the impending movement of the hands or arms (Nashner 1982; see also Marsden et al. 1981). In our experiment, the fingertip touch signal is also eliciting postural responses in the leg musculature to limit center of mass sway. Similarly, Kelso and Tuller (1983) have shown that when movement of a body part is obstructed (e.g., the jaw) during speaking, other body parts can compensate (e.g., lip movement substitutes spontaneously for jaw movement), so that the functional goal of the intended task is accomplished. In fact, adaptive compensations seem to be a general feature of nervous systems. Katz (1950) has reported, for example, that if all six of a beetle's legs are removed, it will use its mandibles for locomotion. Such observations, like ours, mean that the nervous system can plan functional consequences at an abstract level and use multiple effector combinations to bring about the goal, as when one's signature retains its characteristic features when written with either hand or foot.

Acknowledgements The authors thank Joel Ventura and Arthur Larson III for their technical assistance with the force platform and touch apparatus. We would also like to thank Gregor Schöner, Joel Ventura, and Paul DiZio for comments on an earlier version of this paper. J.J. Jeka was supported by NIH postdoctoral fellowship 1 F32 NS09025-01 and J.R. Lackner by NASA grant NAG9-515.

References

- Benson AJ (1982) The vestibular sensory system. In: Barlow HB, Mollon JD (eds) *The senses*. Cambridge University Press, Cambridge, UK, pp 333–368
- Brandt T, Büchele W, Arnold F (1977) Arthrokinetic nystagmus and ego-motion sensation. *Exp Brain Res* 30:331–338
- Burgess PR, Wei JY, Clark FJ, Simon J (1982) Signaling of kinesthetic information by peripheral sensory receptors. *Ann Rev Neurosci* 5:171–187
- Correia MJ, Guedry FE (1966) Modification of vestibular responses as a function of rate of rotation about an Earth-horizontal axis. *Acta Otolaryngol* 62:297–308
- Dichgans J, Brandt T (1973) Visual-vestibular interaction. Effects on self-motion perception and postural control. In: Held R, Leibowitz HW, Teuber HL (eds) *Handbook of sensory physiology*. Springer, Berlin Heidelberg New York 755–804
- Diener HC, Dichgans J, Guschlbauer B, Mau H (1984) The significance of proprioception on postural stabilization as assessed by ischemia. *Brain Res* 296:103–109
- Gordon G (1978) *Active touch. The mechanism of recognition of objects by manipulation: a multi-disciplinary approach*. Pergamon, Oxford
- Gurinkel VS, Levik YS (1994) The suppression of cervico-ocular response by the haptokinetic information about the contact with a rigid, immobile object. *Exp Brain Res*
- Holden M, Ventura J, Lackner JR (1987) Influence of light touch from the hand on postural sway. *Soc Neurosci Abstr* 13 (1):348
- Holden M, Ventura J, Lackner JR (1994) Stabilization of posture by precision contact of the index finger. *J Vest Res* 4:285–301
- Howard IP (1986) The perception of posture, self motion and the visual vertical. In: Boff KR, Kaufmann L, Thomas JP (eds) *Sensory processes and perception*. (Handbook of perception and human performance, vol 1). Wiley, New York, pp 18-1-18-62
- Hullinger M, Nordh E, Thelin A-E, Vallbo ÅB (1979) The responses of afferent fibres from the glabrous skin of the hand during voluntary finger movements in man. *J Physiol (Lond)* 291:233–249
- Johansson RS (1991) How is grasping modified by somatosensory input? In: Humphrey DR, Freund H-J (eds) *Motor control: concepts and issues*. Wiley, New York, pp 331–355
- Johnson KO, Hsiao SS (1992) Neural mechanisms of tactual form and texture perception. *Ann Rev Neurosci* 15:227–250
- Katz D (1950) *Gestalt psychology: its nature and significance*. Ronald, New York
- Kelso JAS, Tuller B (1983) ‘Compensatory articulation’ under conditions of reduced afferent information: a dynamic formation. *J Speech Hear Res* 26:218–223
- Kirk RE (1982) *Experimental design: procedures for the behavioral sciences*. Brooks/Cole, Belmont, Calif
- Knibestöl M (1975) Stimulus-response functions of slowly adapting mechanoreceptors in the human glabrous skin area. *J Physiol (Lond)* 345:63–80
- Lackner JR (1981) Some contributions of touch, pressure and kinesthesia to human spatial orientation and oculomotor control. *Acta Astronautica* 8(8):825–830
- Lackner JR (1992) Multimodal and motor influences on orientation: implications for adapting to weightless and virtual environments. *J Vest Res* 2:307–322
- Lackner JR, Graybiel A (1978a) Some influences of touch and pressure cues on human spatial orientation. *Aviat Space Environ Med* 49:798–804
- Lackner JR, Graybiel A (1978b) Postural illusions experienced during z-axis recumbent rotation and their dependence on somatosensory stimulation of the body surface. *Aviat Space Environ Med* 49:484–488
- Lackner JR, DiZio P (1984) Some efferent and somatosensory influences on body orientation and oculomotor control. In: Wooten R, Spillman L (eds) *Sensory experience, adaptation and perception*. Erlbaum, Hillsdale, NJ, pp 281–301
- Marsden CD, Merton PA, Morton HB (1981) Human postural responses. *Brain* 104:513–534
- Matthews PBC (1981) Evolving views on the internal operation and functional role of the muscle spindle. *J Physiol (Lond)* 320:1–30
- Matthews PBC (1988) Proprioceptors and their contribution to somatosensory mapping: complex messages require complex processing. *Can J Physiol Pharmacol* 66:430–438
- Mauritz KH, Dichgans J, Hufschmidt A (1979) Quantitative analysis of stance in late cortical cerebellar atrophy of the anterior lobe and other forms of cerebellar ataxia. *Brain* 102:461–482
- Nashner LM (1976) Adapting reflexes controlling the human posture. *Exp Brain Res* 26:59–72
- Nashner LM (1981) Analysis of stance posture in humans. In: Towe A, Luschei E (eds) *Motor coordination*. (Handbook of behavioural neurobiology, vol 5) Plenum Press, New York, pp 27–565
- Nashner LM (1982) Adaptation of human movement to altered environments. *Trends Neurosci* 5:358–361
- Phillips CG (1985) *Movements of the hand*. Liverpool University, Liverpool
- Senders V (1958) *Measurement and statistics*. Oxford University Press, New York
- Srinivasan MA, Whitehouse JM, LaMotte RH (1990) Tactile detection of slip: surface microgeometry and peripheral neural codes. *J Neurophysiol* 63(6):1323–1332
- Westling G, Johansson RS (1987) Responses in glabrous skin mechanoreceptors during precision grip in humans. *Exp Brain Res* 66:128–140
- Winter DA, Patla AE, Frank JS (1990) Assessment of balance control in humans. *Med Prog Technol* 16:31–51