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RESEARCH ARTICLE

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The effects of spaceflight on open-loop and closed-loop postural control mechanisms: human neurovestibular studies on SLS-2

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Abstract Stabilogram-diffusion analysis was used to examine how prolonged periods in microgravity affect the open-loop and closed-loop postural control mechanisms. It was hypothesized that following spaceflight: (1) the effective stochastic activity of the open-loop postural control schemes in astronauts is increased; (2) the effective stochastic activity and uncorrelated behavior, respectively, of the closed-loop postural control mechanisms in astronauts are increased; and (3) astronauts utilize open-loop postural control schemes for shorter time intervals and smaller displacements. Four crew members and two alternates from the 14-day Spacelab Life Sciences 2 Mission were included in the study. Each subject was tested under eyes-open, quiet-standing conditions on multiple preflight and postflight days. The subjects' center-of-pressure trajectories were measured with a force platform and analyzed according to stabilogram-diffusion analysis. It was found that the effective stochastic activity of the open-loop postural control schemes in three of the four crew members was increased following spaceflight. This result is interpreted as an indication that there may be in-flight adaptations to higher-level descending postural control pathways, e.g., a postflight increase in the tonic activation of postural muscles. This change may also be the consequence of a compensatory (e.g., "stiffening") postural control strategy that is adopted by astronauts to account for general feelings of postflight unsteadiness. The crew members, as a group, did not exhibit any consistent preflight/postflight differences in the steady-state behavior of their closed-loop postural control mechanisms or in the functional interaction of their open-loop and closed-loop postural control mechanisms. These results are interpreted as indications that although there may be in-flight adaptations to the vestibular system and/or proprioceptive system, input from the visual system can compensate for such changes during undisturbed stance.

Key words Posture · Balance · Center of pressure · Microgravity · Space shuttle · Human

Introduction

Astronauts returning from spaceflight typically exhibit postural difficulties (Homick and Reschke 1977; Homick et al. 1977). A number of dynamic posturographic studies (e.g., Anderson et al. 1986; Kenyon and Young 1986) have shown that these postflight balance instabilities can be related to alterations and/or adaptations to postural control strategies. Moreover, several investigators have demonstrated, in the context of dynamic posturographic investigations, that there are postflight decrements in the function of the vestibular system (Reschke et al. 1984; Young et al. 1984) and proprioceptive system (Roll et al. 1993), respectively. Few static posturographic investigations, however, have demonstrated preflight/postflight differences in the postural sway of astronauts tested under eyes-open conditions. (The poor sensitivity of the majority of these earlier quiet-standing studies, e.g., Paloski et al. 1992b, may have been due, in part, to the fact that the analyses of the posturographic data were limited to summary statistics, which, in general, do not capture the dynamic characteristics of sway patterns.) The only exception we are aware of is the work of Kozlovskaya et al. (1981a,b, 1982). This group found that during postflight posture experiments astronauts exhibit increased levels of lower-limb muscle activity and higher-frequency oscillations in their stabilograms. Nevertheless, further work is needed to understand more completely how in-flight changes to the postural control system affect the regulation of undisturbed stance upon return to the earth's gravitational environment.

In an earlier study (Collins and De Luca 1993), we examined quiet-standing center-of-pressure (COP) trajectories as one-dimensional and two-dimensional ran-

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dom walks. This work was based on the assumption that the movements of the COP represent the combined output of co-existent deterministic and stochastic components. These analyses revealed that over short-term intervals of time during undisturbed stance the COP behaves as a positively correlated random walk, i.e., one which tends to move or drift away from a relative equilibrium point following a perturbation, whereas over long-term intervals of time it resembles a negatively correlated random walk, i.e., one which tends to return to a relative equilibrium point following a perturbation. We interpreted this finding as an indication that during quiet standing the postural control system utilizes open-loop and closed-loop control schemes over short-term and long-term intervals, respectively. (An open-loop control system is one which operates without feedback, whereas a closed-loop control system is one which operates with feedback.) From this perspective, our approach, known as *stabilogram-diffusion analysis*, has the advantage that it leads to the extraction of repeatable COP parameters which can be directly related to the steady-state behavior, e.g., effective stochastic activity, and functional interaction of the neuromuscular mechanisms underlying the maintenance of erect stance.

In the present study, we utilize stabilogram-diffusion analysis and the above postural control model to examine how prolonged periods in microgravity affect the resultant output of the open-loop and closed-loop postural control mechanisms. Specifically, we address three hypotheses concerning the postflight performance and operational characteristics of the "quasi-static" postural control system. Firstly, given the previous reports of increased levels of lower-limb muscle activity during postflight posture experiments (Kozlovskaya et al. 1981a,b), we hypothesize that following spaceflight the effective stochastic activity of the open-loop postural control schemes in astronauts is increased. This hypothesis is based, in part, on the fact that the mean amplitude of the noise-like fluctuations in the force output of a muscle increases as the activity level of the muscle increases (Joyce and Rack 1974). Secondly, given the previous reports of postflight decrements in vestibular (Reschke et al. 1984; Young et al. 1984) and proprioceptive (Roll et al. 1993) function, we hypothesize that the effective stochastic activity and uncorrelated behavior, respectively, of the closed-loop postural control mechanisms in astronauts are increased following spaceflight. Thirdly, given the above postulated changes to the closed-loop postural feedback mechanisms, we hypothesize that following spaceflight astronauts utilize open-loop postural control schemes for shorter time intervals and smaller displacements, i.e., closed-loop postural feedback mechanisms are called into play after shorter delays and smaller drifts in position. We describe how stabilogram-diffusion analysis can be used to test each of these hypotheses.

Materials and methods

Experimental methods

Four crew members (astronauts T, V, W, and Y) and two alternates (control subjects U and Z) from the 14-day Spacelab Life Sciences 2 (SLS-2) Mission were included in the study. All subjects were tested at the Johnson Space Center in Houston, Texas. (This study was approved by the human use committee at the Johnson Space Center.) Postural sway was quantified by using a Kistler 9284 force platform to measure the time-varying displacements of the COP under the subjects' feet. Each subject was instructed to stand in an upright posture in a standardized stance on the platform. In the standardized stance, the subjects' feet were abducted 10° and their heels were separated mediolaterally by a distance of 6 cm. During testing, the subjects stood barefoot with their arms relaxed comfortably at their sides and their eyes open. During the tests, the subjects were instructed to fix their eyes on a point in front of them. (A fixation target was used to control for visual surround and texture, which were constant across trials and across subjects.) Each trial lasted for a period of 30 s and the force platform data were sampled at a frequency of 100 Hz. During each testing session, a series of eight trials was conducted on each subject. Rest periods of 30 s were provided between each trial. The four crew members were tested according to the above posturographic protocol four times prior to the launch date. Three crew members – astronauts V, W, and Y – were tested on four different preflight days (L–120, L–110, L–90, and L–20, where L–X represents a day that was X days prior to launch). The L–120 data for astronaut W were contaminated and therefore not included in the analysis. In order to make up for this lost preflight data, two series of eight posturographic trials were conducted on astronaut W on L–110. Astronaut T was unable to participate in the study until L–90. Consequently, an extra testing session was held for astronaut T on L–68, and two series of eight posturographic trials were conducted on this subject on L–20. The four crew members were also tested according to the above posturographic protocol on four different postflight days (R+1, R+2, R+7, and R+9, where R+X represents the return day plus X days, e.g., R+0 is the day of return and R+1 is the day after return). The two alternates were tested according to the same protocol on three different preflight days (L–120, L–110, and L–90) and one postflight day (R+9).

Stabilogram-diffusion analysis

The COP trajectories were studied as one-dimensional and two-dimensional random walks, according to stabilogram-diffusion analysis (Collins and De Luca 1993). In stabilogram-diffusion analysis, the displacement analysis of COP trajectories is carried out by computing the square of the displacements between all pairs of points separated in time by a specified time interval, Δt. The square displacements are then averaged over the number of Δt making up the COP time series. This process is repeated for increasing values of Δt. A plot of mean-square COP displacement (e.g., $<\Delta r^2>$) versus Δt is known as a "stabilogram-diffusion plot." (In the present study, $\{x_i\}$ and $\{y_i\}$ are the mediolateral and anteroposterior COP time series, respectively, and $<\Delta r^2>=<\Delta x^2>+<\Delta y^2>$. Thus, r designates planar COP measurements and displacements. The brackets <·> denote an average over time or an ensemble average over a large number of samples.) Stabilogram-diffusion plots are computed for each subject trial and then approximately ten such curves are averaged to obtain a resultant stabilogram-diffusion plot for a particular subject. A more complete description of stabilogram-diffusion analysis is given in Collins and De Luca (1993, 1995a).

In order to parameterize resultant stabilogram-diffusion plots, two regions are identified – a short-term region and a long-term region. (Subscripts "s" and "l" will be used throughout the manuscript to denote the short-term and long-term regions, respectively.) These regions are separated by a transition or critical period over which the slope of the stabilogram-diffusion plot changes considerably. Stabilogram-diffusion analysis involves the extraction of three sets of posturographic parameters: diffusion coefficients, scaling exponents, and critical point coordinates.

Diffusion coefficients reflect the level of stochastic activity and/or energy of the COP along the mediolateral or anteroposterior axis or about the plane of support. From a physiological standpoint, the short-term and long-term COP diffusion coefficients characterize the stochastic activity of the open-loop and closed-loop postural control mechanisms, respectively. Diffusion coefficients D_j are calculated from the slopes of the resultant linear-linear plots of mean-square COP displacement versus Δt, according to the general expression:

$$<\Delta j^2>=2D_j\Delta t \tag{1}$$

where $<\Delta j^2>$ is the mean-square COP displacement, and $j=x,y,r$.

Scaling exponents, which can be any real number in the range $0<H_j<1$, quantify the correlation between the step increments making up an experimental time series. If $H_j=0.5$, then the increments in displacement are statistically independent. This is the result expected for classical Brownian motion. If $H_j>0.5$, then past and future increments are positively correlated (Feder 1988; Saupe 1988). In this case, a random walker moving in a particular direction for t_0 will tend to continue in the same direction for $t>t_0$. In general, an increasing (decreasing) trend in the past implies an increasing (decreasing) trend in the future. On the other hand, if $H_j<0.5$, then the stochastic process is negatively correlated (Feder 1988; Saupe 1988). In this case, increasing (decreasing) trends in the past imply, on the average, decreasing (increasing) trends in the future. From a physiological standpoint, COP scaling exponents quantify the correlated behavior of the respective postural control mechanisms, i.e., short-term scaling exponents (which are typically greater than 0.5) characterize the drift-like dynamics of the open-loop postural control mechanisms, whereas long-term scaling exponents (which are typically less than 0.5) characterize the antidrift-like dynamics of the closed-loop postural control mechanisms. Scaling exponents H_j are calculated from the slopes of the resultant log-log plots of mean-square COP displacement versus Δt, according to the generalized scaling law:

$$<\Delta j^2>\sim\Delta t^{2H_j} \tag{2}$$

where the symbols correspond to those of Eq. 1. Diffusion coefficients and scaling exponents are each computed for both the short-term and the long-term regions of resultant stabilogram-diffusion plots. In the present study, the respective slopes needed to calculate these parameters were determined by utilizing the method of least squares to fit straight lines through defined portions of the aforementioned plots. All parameters were determined by a single investigator.

The critical point coordinates – the critical time interval Δt_{jc} and critical mean-square displacement $<\Delta j^2>_c$, where $j=x,y,r$ – approximate the transition region that separates the short-term and long-term regions. An estimate for each critical point was determined as the intersection point of the straight lines fitted to the two regions of the linear-linear version of each resultant stabilogram-diffusion plot. From a physiological standpoint, these coordinates approximate the temporal and spatial characteristics of the region over which the postural control system switches from open-loop control to closed-loop control.

The above approach involves the fitting of two different models (when $H_j\neq0.5$) to the same data sets, i.e., diffusion coefficients representing the slope of a linear model (see Eq. 1), and scaling exponents representing the exponent of a scaling-law model (see Eq. 2). In a recent set of studies (Collins and De Luca 1994, 1995b), we demonstrated that COP trajectories are significantly different from uncorrelated random walks and that the aforementioned (short-range and longer-range) correlations in the COP time series are due to underlying dynamic processes. This result implies that the nonlinear data-analysis technique is more valid than the linear data-analysis technique. Given this result, the COP diffusion coefficients, which are calculated using the linear data-analysis technique, should be viewed as "effective" diffusion coefficients. (Such measures represent "actual" diffusion coefficients only when $H_j=0.5$, which is rarely the case with quiet-standing COP trajectories.) As such, these parameters approximate the effective diffusion of the COP about the base of support. From this perspective and from the standpoint of our postural control hypothesis, the short-term and long-term effective diffusion coefficients should be interpreted as approximate measures of the effective stochasticity of the open-loop and closed-loop control mechanisms, respectively.

Reliability analysis

Intraclass correlation coefficients (ICCs) were calculated to determine the degree of agreement between the respective stabilogram-diffusion parameters that were computed for the crew members on the four preflight testing sessions. The ICC equation for a random effects model, i.e., ICC equation (2,1) as described by Shrout and Fleiss (1979), was used.

Results

The majority of the stabilogram-diffusion parameters demonstrated excellent intersession reliability, i.e., the ICC values were greater than 0.75. The only major exception was the set of long-term scaling exponents, which had low ICC values. This result can be attributed to the fact that the intrasubject variability of the respective long-term scaling exponents was large relative to their intersubject variability.

To test the hypothesis that the effective stochastic activity of the open-loop postural control mechanisms in astronauts is increased following spaceflight, we examined the computed pre- and postflight values of the short-term effective diffusion coefficients (Fig. 1) for the four crew members and two alternates. It can be seen from Fig. 1 that the short-term effective diffusion coefficients for three of the crew members (astronauts T, V, and W) exhibited a postflight increase, i.e., the slopes of the short-term region of their linear-linear plots of mean-square COP displacement versus time interval were larger immediately following spaceflight (see Fig. 2). By R+9, these parameters returned to their preflight baseline levels. We also examined the computed pre- and postflight values of the short-term scaling exponents for the above subjects. The crew members, as a group, did not exhibit any consistent preflight/postflight differences in the values of their short-term scaling exponents. However, it should be noted that the COP trajectories for the crew members behaved as positively correlated random walks ($H_{js}>0.5$) over short-term intervals of time, as was found in our earlier studies of healthy young subjects (Collins and De Luca 1993, 1994, 1995a,b).

To test the hypothesis that the effective stochastic activity and uncorrelated behavior of the closed-loop postural control mechanisms in astronauts are increased following spaceflight, we examined the computed pre- and postflight values of the long-term effective diffusion coefficients and scaling exponents, respectively, for the four crew members and two alternates. Firstly, the crew members, as a group, did not exhibit any consistent preflight/postflight differences in the values of their long-term effective diffusion coefficients. The postflight values of the long-term anteroposterior effective diffusion coefficient for one crew member (astronaut W) were

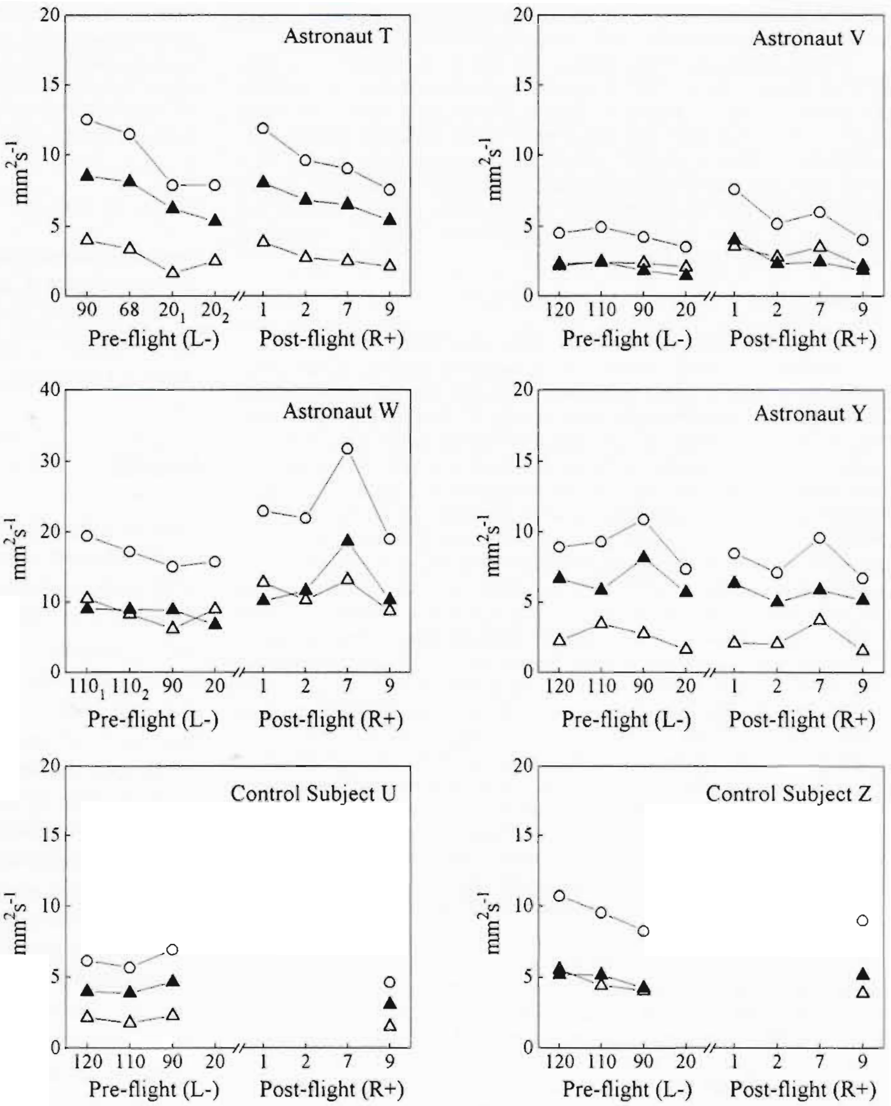

Fig. 1 The computed pre- and postflight values of the short-term effective diffusion coefficients for the four crew members (astronauts T, V, W, and Y) and two alternates (control subjects U and Z). The short-term effective diffusion coefficients for three of the crew members (astronauts T, V, and W) exhibited a postflight increase. By postflight day 9 (R+9), these parameters returned to their preflight baseline levels. *Empty triangles*, short-term effective diffusion coefficients, mediolateral (D_{xs}); *filled triangles*, short-term effective diffusion coefficients, anteroposterior (D_{ys}); *empty circles*, short-term effective diffusion coefficients, planar (D_{rs})

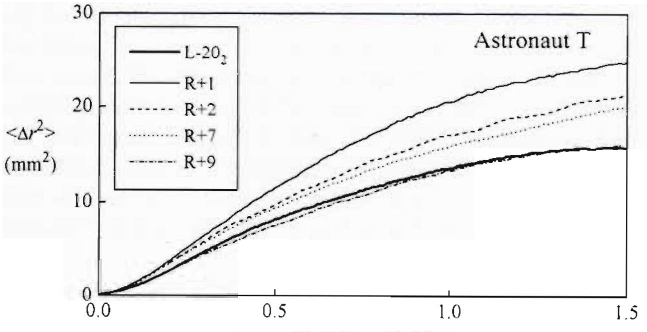

Fig. 2 Magnified views of the short-term region (and the initial portion of the long-term region) of the raw-data resultant linear-linear plots of mean-square planar center-of-pressure displacement versus time interval for a representative crew member (astronaut T) for one preflight testing session (L–20$_2$) and the four postflight testing sessions ($\langle \Delta r^2 \rangle$)

generally smaller than those for preflight. (Similar changes were found in this subject's long-term planar effective diffusion coefficient. It should be pointed out, however, that changes in planar stabilogram-diffusion parameters, e.g., D_{rl}, are directly related to changes in the respective anteroposterior and/or mediolateral parameters.) However, a similar decrease in D_{yl} was found in the "postflight" results for control subjects U and Z. Secondly, the crew members, as a group, did not exhibit any consistent preflight/postflight differences in the values of their long-term scaling exponents. Nonetheless, it should be noted that the COP trajectories for the crew members behaved as negatively correlated random walks ($H_{jl}<0.5$) over long-term intervals of time, as was found in our earlier studies of healthy young subjects (Collins and De Luca 1993, 1994, 1995a,b).

To test the hypothesis that following spaceflight astronauts utilize open-loop postural control schemes for shorter intervals of time and smaller displacements, we examined the computed pre- and postflight values of the critical time intervals and critical mean-square displacements, respectively, for the four crew members and two alternates. Firstly, the crew members, as a group, did not exhibit any consistent preflight/postflight differences in the values of their critical time intervals. However, the critical time intervals for one crew member (astronaut T) exhibited a slight postflight increase, whereas those for another crew member (astronaut W) exhibited an equivalent postflight decrease. Secondly, the crew members, as a group, did not exhibit any consistent preflight/postflight differences in the values of their critical mean-square displacements. However, two of the three crew members who exhibited a postflight increase in their short-term effective diffusion coefficients (astronauts T and V) also exhibited a postflight increase in their critical mean-square displacements. These results were not unexpected given that the critical mean-square displacement for a subject should increase if that subject's short-term effective diffusion coefficient increases and his or her critical time interval either increases or remains unchanged. (The postflight decrease in the critical time intervals for astronaut W largely offset the effects of the postflight increase in this subject's short-term effective diffusion coefficients.)

Discussion

The results of the present study supported the hypothesis that the effective stochastic activity of the open-loop postural control mechanisms in astronauts is increased following prolonged periods in microgravity. Specifically, we showed that three of the four SLS-2 astronauts exhibited larger short-term effective diffusion coefficients during the initial postflight testing sessions. It is possible that such changes are the direct result of in-flight adaptations to the postural control system. For instance, these effects may be the result of changes in higher-level descending postural control pathways, e.g., a postflight increase in the tonic activation of postural muscles. However, it is also possible that these alterations are the consequence of a compensatory postural control strategy that is adopted by crew members to account for general feelings of unsteadiness, which may be related to other in-flight postural adaptations. In particular, the aforementioned changes in short-term effective diffusion coefficients may be the result of a compensatory strategy wherein astronauts increase the stiffness of their musculoskeletal systems by increasing the level of muscular activity across the joints of their lower limbs. Since fluctuations are always present in the mechanical output of skeletal muscles (De Luca et al. 1982) and since the mean amplitude of these noise-like fluctuations increases as the amount of force produced by a muscle increases (Joyce and Rack 1974), the above compensatory strategy would lead to larger average levels of short-term postural sway and larger short-term effective diffusion coefficients, as were calculated for three of the four crew members. Both of these interpretations are indirectly supported by the work of Kozlovskaya et al. (1981a,b), who, as noted earlier, found that astronauts exhibit increased levels of lower-limb muscle activity during postflight posture experiments. Unfortunately, the collection of electromyographic data was not part of our protocol.

It is also possible that the aforementioned parameter changes may be the direct result of in-flight changes to muscle dynamics and/or function. S. Roy et al. (personal communication), for instance, have shown that lower-limb muscle function (i.e., static strength and endurance) is impaired in humans following prolonged periods in microgravity. Immediately following spaceflight, the amplitude of the noise-like fluctuations in the force output of postural muscles (at force levels appropriate for quiet standing) may be increased. Such a change would lead to larger short-term effective diffusion coefficients. Unfortunately, the above measure of muscle performance was not considered by Roy et al. (personal communication). This issue requires further study.

Our present findings did not support the hypothesis that the effective stochastic activity and uncorrelated behavior, respectively, of the closed-loop postural control mechanisms in astronauts are increased following prolonged periods in microgravity. The crew members, as a group, did not exhibit any consistent preflight/postflight differences in the values of their long-term effective diffusion coefficients or scaling exponents, respectively. Our computed results also did not support the hypothesis that following spaceflight astronauts utilize open-loop postural control schemes for shorter time intervals and smaller displacements. The crew members, as a group, did not exhibit any consistent preflight/postflight differences in the values of their critical point coordinates. We interpret these results as indications that although there may be in-flight adaptations to the vestibular system (Reschke et al. 1984; Young et al. 1984) and/or proprioceptive system (Roll et al. 1993), input from the visual system can compensate for such changes during undisturbed stance. (It is possible that in-flight changes to the vestibular system and/or proprioceptive system would be manifested during quiet standing if visual input were selectively removed, i.e, if the astronauts were tested under eyes-closed conditions. The SLS-2 astronauts were not tested under eyes-closed conditions using the present posturographic protocol because of schedule constraints.) This interpretation is consistent with the reported finding that astronauts have an increased reliance on visual input during postflight dynamic-posturographic/orientation experiments (Young et al. 1984, 1986; Anderson et al. 1986; Kenyon and Young 1986; Paloski et al. 1992b; D. Merfeld, personal communication).

The above negative results should be interpreted with caution, however, given that the first postflight testing session was not held until R+1. It is possible that the time course for readaptation for many (undetected) in-flight changes relevant to quiet-standing dynamics may be less than 24 h. Paloski et al. (1992a), for instance, found that a considerable amount of neurosensory readaptation occurs within the first 10–12 h after landing. Similar findings have been reported for the otolith-spinal system (Watt et al. 1986). In contrast with these studies, it is interesting to note that the present results suggest that spaceflight-related changes which affect the resultant output of open-loop postural control mechanisms may have a considerably slower time course for readaptation, i.e., these changes have a demonstrable effect on the performance of the quasi-static postural control system for several days postflight.

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