doi:10.1093/brain/awm157 Brain (2007), 130, 2097–2107

Equilibrium during static and dynamic tasks in blind subjects: no evidence of cross-modal plasticity

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Can visual information be replaced by other sensory information in the control of static and dynamic equilibrium? We investigated the balancing behaviour of acquired and congenitally blind subjects (25 severe visually impaired subjects—15 males and 10 females, mean age 36 ± 13.5 SD) and age and gender-matched normal subjects under static and dynamic conditions. During quiet stance, the centre of foot pressure displacement was recorded and body sway analysed. Under dynamic conditions, subjects rode a platform continuously moving in the antero-posterior direction, with eyes open (EO) and closed (EC). Balance was inferred by the movement of markers fixed on malleolus, hip and head. Amplitude of oscillation and cross-correlation between body segment movements were computed. During stance, in normal subjects body sway was larger EC than EO. In blind subjects, sway was similar under both visual conditions, in turn similar to normal subjects EC. Under dynamic conditions, in normal subjects head and hip were partially stabilized in space EO but translated as much as the platform EC. In blind subjects head and hip displacements were similar in the EO and the EC condition; with respect to normal subjects EC, body displacement was significantly larger with a stronger coupling between segments. Under both static and dynamic conditions, acquired and congenitally blind subjects had a similar behaviour. We conclude that long-term absence of visual information cannot be substituted by other sensory inputs. These results are at variance with the notion of compensatory cross-modal plasticity in blind subjects and strengthen the hypothesis that vision plays an obligatory role in the processing and integration of other sensory inputs for the selection of the balancing strategy in the control of equilibrium.

Keywords: sensorimotor control; control of posture; vision; blindness; cross-modal plasticity

Abbreviations: EO = eyes open; EC = eyes closed

Received February 13, 2007. Revised May 22, 2007. Accepted June 14, 2007. Advance Access publication July 4, 2007

Introduction

The control of human stance depends upon the integration of information from diverse sensory modalities. Modifications of visual environment (Mergner *et al*., 2005) or of proprioception (Bove *et al*., 2003; Schieppati *et al*., 2003) or enhanced or impaired cutaneous inflow (Kavounoudias *et al*., 1998) or changes in vestibular input (Day *et al*., 1997; Bacsi and Colebatch, 2005) are all able to produce postural instability.

Vision plays a paramount role in the coding and processing of other sensory information (Paulus *et al*., 1984). With eyes closed, stability is reduced during quiet stance (Dichgans *et al*., 1976; Schieppati *et al*., 1999) as well as in dynamic postural tasks (Gurfinkel *et al*., 1975; Buchanan and Horak, 1999; Corna *et al*., 1999). In a specific dynamic task like riding a mobile platform periodically translating in the horizontal plane, visual information triggers a robust balancing strategy, whereby subjects partially stabilize their head in space with eyes open, while the head oscillates as much as or more than the platform with eyes closed (Buchanan and Horak, 1999; Corna *et al*., 1999; Schieppati *et al*., 2002; De Nunzio *et al*., 2007). Therefore, under both quiet stance and dynamic conditions, vision is not readily replaced by other sensory inputs in normal subjects. However, it remains unclear if and to what extent one or more sensory modalities can replace vision through long-term plasticity.

There is a general consensus on the idea that, compared to the sighted population, blind subjects develop higher abilities in the use of their remaining senses (the compensatory hypothesis, Rauschecker, 1995a; see Pascual-Leone *et al.*, 2005) in tasks implicating touch and hearing (Lessard *et al.*, 1998; Roder *et al.*, 1999; Van Boven *et al.*, 2000; Goldreich and Kanics, 2003; Gougoux *et al.*, 2004; Voss *et al.*, 2004). Evidence of brain plasticity in blind subjects leads to conclude that the brain areas commonly associated with the processing of visual information are recruited in a compensatory cross-modal manner that may account for their superior capacities (Cohen *et al.*, 1997; Bavelier and Neville, 2002; Theoret *et al.*, 2004). However, given the relevance of vision in tasks implying control of equilibrium (Peterka and Loughlin, 2004), the hypothesis that loss of sight cannot be compensated and is instead detrimental to appropriate integration and processing of other afferent inputs for postural control cannot be excluded (the general-loss hypothesis, see Pascual-Leone *et al.*, 2005). When postural control was tested providing blind subjects with additional sensory information like haptic cues or auditory cues (Jeka *et al.*, 1996; Easton *et al.*, 1998), no superior abilities with respect to sighted subjects with eyes closed were demonstrated.

To get insight in favour of the compensatory or of the general-loss hypothesis, we investigated the balancing behaviour of blind subjects during both quiet stance and riding a mobile platform. Our aims were to assess whether they reduce body oscillation based on their past experience and acquired skill in the use of their remaining sensory information, and whether acquired blind behave like congenitally blind subjects, in whom the plasticity process would be differently structured. The results show that balance behaviour was definitely not superior in blind than in normal subjects and argue against the exploitation of cross-modal plasticity in the control of either static or dynamic balance.

Materials and Methods

Experimental subjects

Experiments were performed in two laboratories (the Human Movement Laboratory at Pavia and the Posture and Movement Laboratory at Veruno, both belonging to the Scientific Institute Fondazione Salvatore Maugeri), in order to enlarge the patient population and test different platform translation patterns. Twenty-five severe visually impaired subjects (henceforth referred to as blind subjects) participated in this study (15 males and 10 females, mean age 36 ± 13.5 SD). The cause of the visual impairment included retinopathy of prematurity, congenital glaucoma, optic nerve abnormalities, retinitis pigmentosa, brain injury, congenital cataract, chiasm astrocytoma, bilateral retinal detachment, Leber's amaurosis. No subject had deficits in other sensory systems. The visual impairment was of congenital (13 subjects) or of acquired nature. To evaluate the severity of vision loss based on visual acuity (visus), all subjects had undergone an ophthalmological examination. The residual visual acuity was measured following the ETDRS testing protocol (Early Treatment for Diabetic Retinopathy Study, National Eye Institute, National Institutes of Health, USA). All subjects had visus values <0.08 (0.05 ± 0.03). No subject used to wear corrective refractive lenses. All had undergone formal orientation and mobility training. The control group was composed by 25 normal-sighted subjects (13 males and 12 females, mean age 43 years $\pm$ 5.9), all with visus values between 0.9 and 1 with their usual visual correction where applicable. All subjects gave written informed consent to participate in the study, which was performed according to the Declaration of Helsinki and the guidelines of the local ethics committee. All blind and normal subjects were naïve to the experimental procedures.

Quiet stance

Six stance trials were recorded in each subject under eyes open (EO) and eyes closed (EC) conditions. Each trial lasted 51 s, during which subjects were asked to stand upright in a natural position (feet spaced 10 cm), with arms by their side. The experimental room was well illuminated and subjects were surrounded by patterned walls. Visual conditions were randomized across trials. The three components of the force (F_x, F_y, F_z) acting on a stabilometric platform (AMTI, USA or Kistler, CH) were sampled at 10 Hz, and from these variables a program calculated the instantaneous centre of foot pressure (CFP). Since quiet stance is accompanied by omnidirectional sway, balance assessment was carried out by computing the length of the path travelled by CFP on the horizontal plane (sway path). This variable takes into account body sway along both A–P and M–L directions.

Dynamic task

This consisted in riding a mobile platform (Lomazzi & Co. and e-TT, Italy), periodically translating in the antero-posterior (A–P) direction on the horizontal plane in a sinusoidal fashion. The subjects studied in Veruno (16 normal and 16 blind subjects) performed the task at a translation frequency of 0.2 and 0.6 Hz, with oscillation amplitude of 6 cm peak-to-peak (*Protocol 1*). The subjects studied in Pavia (9 normal and 9 blind subjects) performed the task at 0.5 Hz and 10 cm peak-to-peak amplitude (*Protocol 2*). Buchanan and Horak (1999) and Corna *et al.* (1999) examined changes in behaviour for translation frequencies below and above 0.5 Hz, pointing to substantial differences in balancing strategy. Therefore, the three complementary platform translation protocols have been used with the aim of generalizing the conclusions of the present study. The characteristics of the platform perturbations were deliberately chosen to minimize the risk of falling and to avoid the use of a harness that would have triggered additional sensory information. All subjects stood on the moving platform, in a natural position (feet spaced 10 cm), with the arms by their side and looked at a patterned wall. After one tryout (15 s EO, 15 s EC) for familiarizing with the platform oscillations, two to four trials for each visual condition depending on the subject's compliance were acquired. EO and EC trials were randomized within each subject. Each trial lasted 30 s. The initial 10 s were not analysed in order to avoid the transitory events due to the onset of the platform movement. When necessary, subjects rested between trials. To reduce the faint noise produced by the platform motors, subjects were wearing a headphone. Reflective markers were placed on the vertex (head), greater trochanter (hip) and malleolus (invariable with respect to the moving platform). Kinematics data were acquired by means of optoelectronic devices (CoSTEL, LOG.IN, Italy and ELITE, BTS, Italy) and were automatically subjected to interpolation by the motion analysis software. Body segment movements acquired during the dynamic task were assessed by calculating the A–P displacements of head and hip, since displacements in the A–P direction largely overcome any M–L movement. As an index of the average amplitude of the segment displacement in the sagittal plane, the standard deviation (SD) of head and hip markers' traces over time was computed (Corna *et al.*, 1999). This is influenced both by the periodic peak-to-peak body displacements directly linked to the platform movement and by any other displacement or drift of body segments during the balancing behaviour, not directly connected with the pattern of platform oscillation. For comparison, the SD of the trace of the malleolus marker gave the reference value of the platform movement.

In order to estimate the degree of coupling between the moving body segments, the cross-correlation (CC) functions between the traces of head and malleolus markers and of head and hip markers were calculated. The analysis gave a correlation coefficient (R) dependent on the strength of the association between the segments' periodic movements. A positive R value indicated that the displacement was in the same sense (both segments moved forward or backward); a negative value indicated movement in opposite sense. The time lag between the periodic displacement of head and malleolus was also computed. A time lag equal to zero indicated in-phase displacement of the head and a positive time lag indicated a delay of the head with respect to the moving platform displacement.

Statistical analysis

When not otherwise stated, results are expressed as mean $\pm$ SD. In both static and dynamic tasks, for each subject the mean value of all individual trials performed under the same condition were considered. For the CC analysis, R-values were transformed in z-scores [$z = 1/2 \ \ln \ (1+R)/(1-R)$]. These ranged from 0 to about 3, corresponding to R-values of 0 and 0.99, respectively.

For stabilometric variables, a two-way ANOVA (normal/blind as between groups factor and visual condition as within-group factor) was computed. For the dynamic task of *Protocol 1*, a four-way ANOVA was used to analyse the SD of head and hip A–P displacement, with normal/blind as between-group factors and frequency, visual condition and body segment as within-group factors (repeated measures). A three-way ANOVA (normal/blind, with frequency and visual condition as repeated measures) was used to analyse the z-score and the time-lag data. For *Protocol 2*, since only one platform oscillation frequency was used, a three-way ANOVA (normal/blind, with visual condition and body segment as repeated measures) was applied on the SD of head and hip displacement, and a two-way ANOVA (normal/blind, with visual condition as repeated measures) was applied on z-score and the time-lag data. When data of acquired and congenitally blind subjects were compared, a two-way ANOVA (acquired/congenital as between-group factor with visual condition as repeated measures) was used for both static and dynamic tasks. When the results of the ANOVA were significant ($P < 0.05$), the Newman–Keuls *post hoc* test was run.

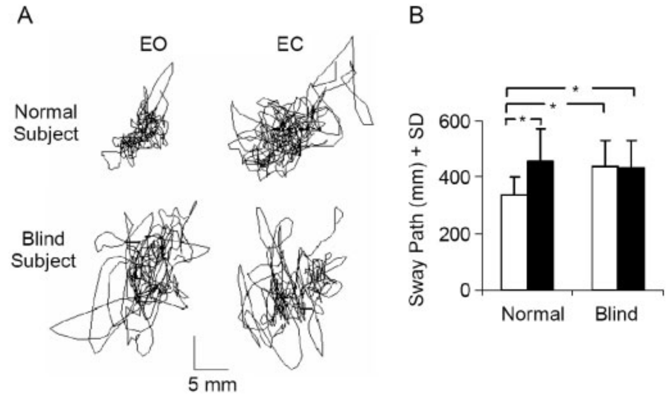

Fig. 1 (**A**) Example of stabilometric recordings during quiet stance in a normal and in a blind representative subject with EO and EC. (**B**) Mean sway path (+SD) in normal and blind subjects under the two visual conditions. The differences between EO and EC condition, clearly visible in normal subjects, disappear in blind subjects.

Results

Quiet stance

Examples of stabilometric recording under EO and EC conditions in a normal and a blind representative subject is shown in panel A of Fig. 1. The different amplitude between visual conditions of the surface covered by the movement of the CFP is obvious in the normal subject, but disappears in the blind subject. During quite stance, the blind subject's behaviour with EO closely reproduced that with EC. In turn, this behaviour was similar to that of the normal subject with EC.

The average sway path for all normal subjects and all blind subjects under the two visual conditions is reported in panel B of Fig. 1. The two-way ANOVA showed different values between visual conditions ($F = 37.36$ df $= 1$, 48; $P < 0.0001$) and an interaction between group and visual condition ($F = 42.16$, df $= 1$, 48; $P < 0.0001$). The *post hoc* test showed that the mean sway path was larger in EC than EO condition in normal subjects ($P < 0.0002$). On the contrary, in the blind subjects the mean sway path remained similar in both visual conditions ($P > 0.7$). These mean values were different from the sway path of normal subjects EO ($P < 0.001$, for all comparisons), but comparable with that of normal subjects EC ($P > 0.1$, for all comparisons). In normal subjects the mean Romberg quotient (the ratio of sway path EC/EO) was equal to 1.39 ± 0.24, whereas in blind subjects it was equal to 0.99 ± 0.14 (t-test for independent samples: $P < 0.0001$).

Dynamic task

Protocol 1 (0.2 and 0.6 Hz, 6 cm)

Normal as well as blind subjects were able to perform the required task, regardless of the eyes being opened or closed. No subject ever fell over or made a step to maintain the equilibrium during the trials. Figure 2A shows examples of

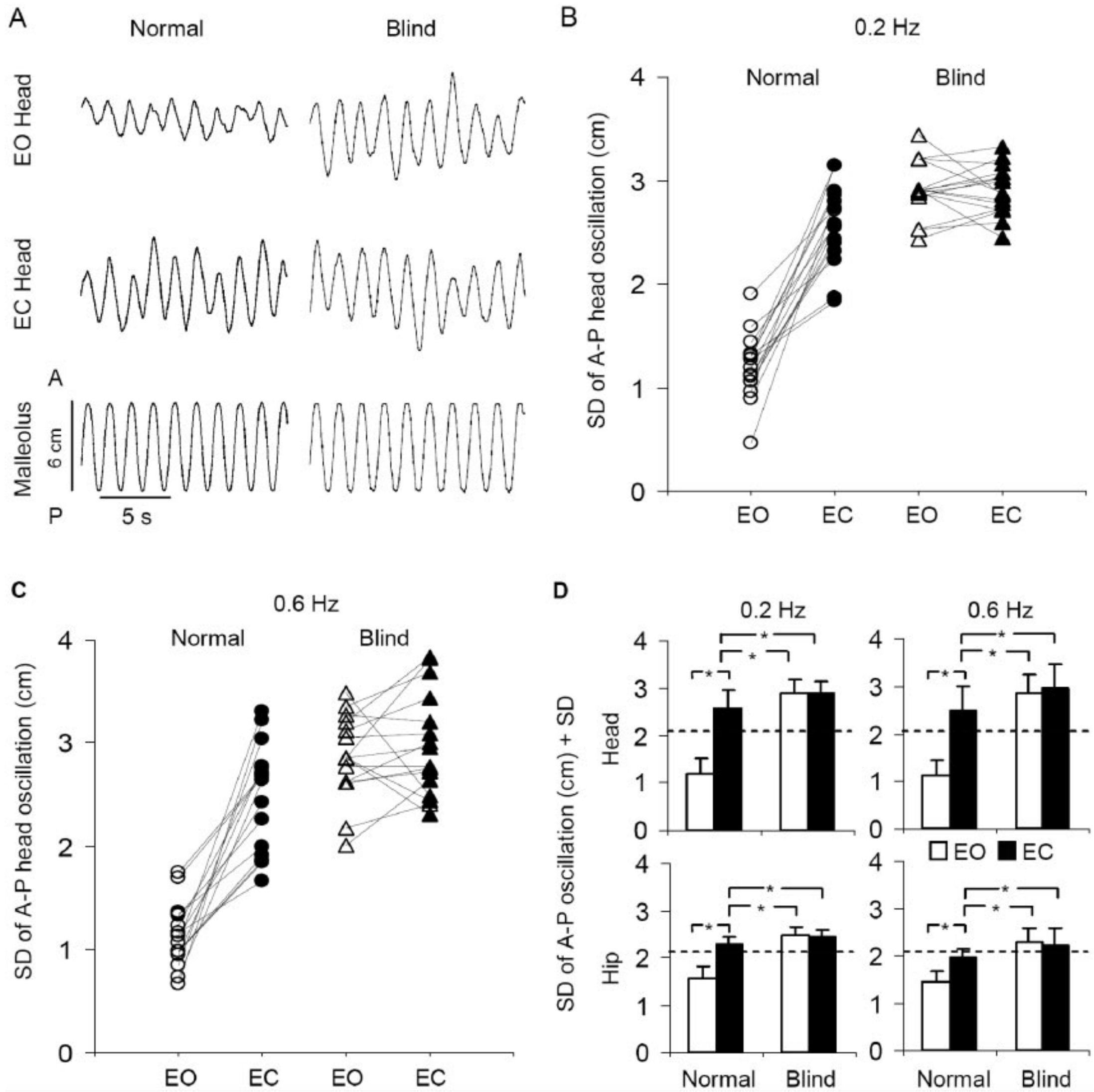

Fig. 2 (**A**) Example of A–P oscillation of head and malleolus markers obtained during stance with EC and EO on the continuously moving platform at 0.6 Hz and 6 cm peak-to-peak displacement 0in a normal and a blind subject. The amplitude of the head oscillation of the blind subject is comparable in the two visual conditions and is quite similar to that of normal subject with EC. (**B–C**) The mean values of the SD of the A–P head displacement of each normal and each blind subject are superimposed. (**D**) Mean of the standard deviation (SD) of head and hip oscillations along the A–P axis (+SD) under EO and EC condition for both normal and blind subjects. The horizontal dashed line indicates the SD of A–P oscillation of malleolus (invariable with respect to the moving platform). In spite of the frequency used, blind subjects do not show different behaviour in the trials performed with EO and with EC.

the traces of the head marker movements of a normal and a blind subject, in the two visual conditions. The traces of the malleolus marker (fixed with respect to the platform) are also depicted (bottom trace). The normal subject tended to stabilize the head in space with EO, whereas the head oscillated like the platform with EC. The blind subject behaved very much in the same way with eyes open and closed: they followed the platform oscillations with the entire body, head included, under both visual conditions. This behaviour was in turn similar to that of the normal subject performing the task with EC.

The mean values of the SD of the A–P displacement of the head of each normal and blind subject for each visual condition are shown in Fig. 2B and C, for the 0.2 and 0.6 Hz platform translation frequencies, respectively. Figure 2D shows a summary of the mean group data for head and hip oscillation, separated for platform frequency, visual condition and body segment. Four-way ANOVA showed differences in the mean values of the SD of head and hip displacement between groups ($F = 186.42$, df = 1, 30; $P < 0.0001$), frequency ($F = 6.06$, df = 1, 30; $P < 0.02$), visual condition ($F = 92.28$, df = 1, 30; $P < 0.0001$) and body segment ($F = 78.92$, df = 1, 30; $P < 0.0001$). The *post hoc* test showed that in normal subjects at both 0.2 and 0.6 Hz the oscillations of head and hip were significantly reduced in EO compared to EC condition

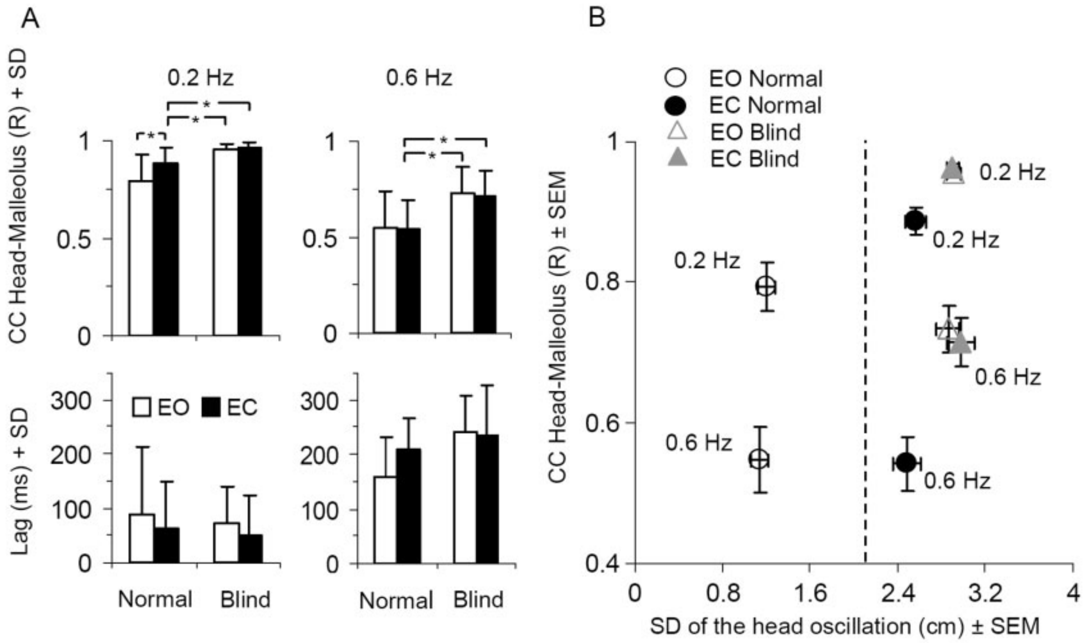

Fig. 3 (**A**) Upper panels: mean cross correlation values (+SD) between head and malleolus traces. For both normal and blind subjects the CC is reduced at 0.6 Hz with respect to 0.2 Hz. Blind subjects show higher CC values with respect to normal subjects. (**A**) Bottom panels: the mean values of time lag (+SD) between head and malleolus traces are greater at 0.6 than 0.2 Hz. (**B**) Relationship between malleolus and head traces CC and SD values of A–P head oscillation, at 0.2 and 0.6 Hz. The vertical dashed line indicates the SD of A–P oscillation of malleolus. At 0.2 Hz blind subjects' behaviour was characterized by large head A–P oscillation (high SD), with a strong association between head and platform (high CC), regardless of the visual condition. At 0.6 Hz, in spite of similar head oscillation, the CC decreases. Overall, blind subjects exhibited greater CC values and larger head oscillations than normal subjects.

($P<0.001$ for all comparisons). Furthermore, for both frequencies tested, the head oscillated more than the hip with EC ($P<0.002$ for all comparisons), whereas the hip oscillated more than the head with EO ($P<0.001$). In the blind subjects, independently of visual condition and platform oscillation frequency, the head oscillated more than the hip ($P<0.001$ for all comparisons). Therefore, the strategy used by blind subjects was very similar to that of the normal subjects EC. Nevertheless, in blind subjects, both with EO and EC, head and hip oscillated significantly more than that of the normal subjects EC ($P<0.001$ for both 0.2 and 0.6 Hz). The effects of the two frequencies on head and hip kinematics were also checked. In normal subjects, there were no major effects on oscillation amplitudes ($P>0.2$ for both comparisons, except for hip EC, smaller at 0.6 Hz, $P<0.001$). The same was true for blind subjects.

The CC between the traces of head and malleolus was computed for both normal and blind subjects in the two visual conditions. The mean head–malleolus CC coefficients for normal and blind subjects, and for both frequencies and both visual conditions, are shown in Fig. 3A. Three-way ANOVA computed on the *z*-score showed different values between groups ($F=43.52$, df$=1$, 30; $P<0.0001$) and between frequencies ($F=251.90$, df$=1$, 30; $P<0.001$) and an interaction between frequency and vision ($F=14.29$, df$=1$, 30; $P<0.015$). In normal subjects, the *post hoc* test showed that the *z*-score was lower EO than EC at 0.2 Hz ($P<0.001$). This difference was absent at 0.6 Hz. In the blind subjects, the mean *z*-score values were similar between the two visual conditions for both frequencies tested. When the results of the two groups were compared, the mean *z*-score of the blind subjects was always higher than that of the normal subjects ($P<0.0001$, for all comparisons) regardless of frequency and visual condition. Overall, this finding points to a somewhat stronger coupling between head and feet in the blind than in the normal subjects. Comparing the results obtained at the two different platform oscillation frequencies, within each visual condition, the *z*-score was smaller at 0.6 than at 0.2 Hz, for both subject groups ($P<0.0001$, for all comparisons).

Figure 3B shows the indexes of segment association (the head–malleolus CC values) and of head oscillation (the head SD) to form a synthetic illustration of the behaviour adopted by normal and blind subjects. At 0.2 Hz, the blind subjects' behaviour was characterized by large SDs of the head oscillation, with a good compliance (high CC) with the perturbing platform movement, regardless of the visual condition. At 0.6 Hz, in spite of similar head oscillation, the CC decreased in both normal and blind subjects. Overall, blind subjects exhibited greater CC values and larger head oscillations than normal subjects. For the blind subjects, this behaviour was the same under EO and EC conditions.

The analysis of the CC between the displacements of head and hip gave results (not shown in figure)

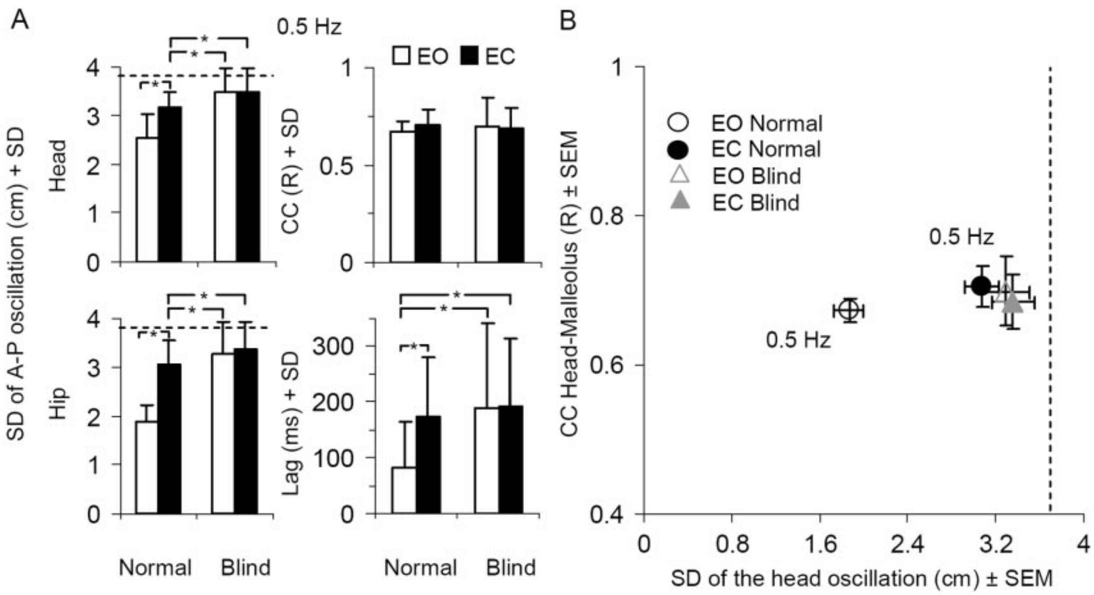

Fig. 4 (**A**) Mean values of the SD of the head and hip oscillations along the A–P axis (+SD) (upper and bottom left panels). The horizontal dashed line indicates the SD of A–P oscillation of malleolus. The amplitude of head and hip oscillations never overshot that of the platform. The blind subjects behaved in similar way when they perform the task with EO and EC. This behaviour was similar to that of normal subjects with EC. The mean cross correlation values and the mean time lag value (+SD) between head and malleolus traces are also showed (upper and bottom right panels). The CC values of blind subjects are comparable to that of normal subjects. (**B**) Relationship between malleolus and head traces CC and SD values of the A–P oscillation of the head. The vertical dashed line indicates the SD of A–P oscillation of malleolus. Blind subjects exhibited comparable SD of head oscillation and comparable CC between the two visual conditions.

not much different from the CC between head and malleolus. The three-way ANOVA computed on the mean *z*-score showed different values between groups ($F = 48.62$, df = 1, 30; $P < 0.001$), frequencies ($F = 231.78$, df = 1, 30; $P < 0.001$) and visual conditions ($F = 15.97$, df = 1, 30; $P < 0.001$). There was an interaction between group and frequency ($F = 10.44$, df = 1, 30; $P < 0.01$) and group and vision ($F = 14.29$, df = 1, 30; $P < 0.015$). In normal subjects, the *post hoc* test showed that the *z*-score was lower with EO than EC ($P < 0.01$ at both frequencies). In the blind subjects, the *z*-score were similar between the two visual conditions for both frequencies. When the results of the two groups were compared, the *z*-score value of the blind subjects was always higher than that of the normal subjects (significantly so at 0.2 Hz, $P < 0.01$ for both EO and EC).

The time lags between head and malleolus, which represent an index of the temporal association between these two body segments, are summarized in the bottom panel of Fig. 3A. For both groups and both translation frequencies, the head just failed to keep pace with the platform movement. This delay was greater at 0.6 than 0.2 Hz. The three-way ANOVA showed no difference in time lag between normal and blind subjects. An effect was present only for frequencies ($F = 95.77$, df = 1, 30; $P < 0.0001$). The *post hoc* test confirmed that for both groups of subjects and independently of the visual condition, the mean time lag at 0.6 was greater than at 0.2 Hz ($P < 0.005$ for all comparisons). No significant relationship between CCs and time lags was found either across normal or blind subjects, or when all the normal and blind subjects were pooled.

Protocol 2 (0.5 Hz, 10 cm)

These blind subjects showed basically equivalent results as those taking part in *Protocol 1*. All variables showed the same qualitative features and differences with respect to the normal subjects, as those reported for *Protocol 1*. This was true in spite of the different values of the body segment oscillations connected with the different platform oscillation pattern. This notwithstanding, there were no differences in the spatial and temporal patterns of head and hip oscillation between EO and EC in the blind subject group (Fig. 4A, upper and bottom left panels). Three-way ANOVA showed differences between groups ($F = 14.99$, df = 1, 16; $P < 0.002$), visual conditions ($F = 24.29$, df = 1, 16; $P < 0.0005$) and body segments ($F = 10.21$, df = 1, 16; $P < 0.005$). The interaction between groups and visual conditions was significant ($F = 20.36$, df = 1, 16; $P < 0.0005$). Specifically, in blind subjects, both EO and EC, the head and hip oscillations were larger with respect to the EC condition of normal subjects ($P < 0.0008$ for all comparisons).

The mean head–malleolus CC coefficients for normal and blind subjects and for each visual condition are shown in the upper right panel of Fig. 4A. The two-way ANOVA computed on the mean *z*-score showed no differences between groups and between visual conditions. When the head–hip CC was analysed (not shown in the figure), ANOVA showed no difference between groups; there was a difference between visual conditions ($F=9.35$, df$=1$, 16; $P<0.01$) and an interaction between group and vision ($F=7.50$, df$=1$, 16; $P<0.05$). In normal subjects, the *post hoc* test showed that the *z*-score was lower with EO than EC ($P<0.001$). In blind subjects, the *z*-score was similar between the two visual conditions. When the results of the two groups were compared, the *z*-score of the blind subjects was always higher than that of the normal subjects (significantly so only for the EO condition, $P<0.01$). Two-way ANOVA for the mean time lag values (bottom right panel of Fig. 4A) showed results close to significance level for visual conditions ($F=3.94$, df$=1$, 16; $P=0.06$) but not for groups.

In Fig. 4B, the head–malleolus CC values are plotted against the SD of head oscillation for different visual conditions. The blind subjects' behaviour was characterized by larger head A–P oscillations than that of normal subjects EC, being the same regardless of the visual condition. As for Protocol 1, no significant relationship was found across normal or blind subjects, or all subjects pooled, between CCs and time lags.

Comparison between balancing behaviour in blind subjects of congenital and acquired origin

There were 13 congenital blind subjects, with a mean age of 33.8 years ± 14.9. The mean age of the 12 acquired blind subjects was 31 ± 8.9. The mean duration of acquired blindness was 14.7 years ± 9.0 SD. Under quiet stance condition, there were no differences between these two sub-groups in sway path. When the comparison between sub-groups was carried out on the body segment oscillation data obtained during the dynamic task, we tested separately the results of *Protocol 1* (eight congenital and eight acquired) and *Protocol 2* (five congenital and four acquired). The head and hip oscillations at 0.6 Hz showed comparable values between the two sub-groups of congenital and acquired blind subjects. Overall, the comparisons gave similar results also for the 0.2 Hz translation frequency. Also for *Protocol 2*, head and hip oscillations showed comparable values between the two sub-groups.

Discussion

This study compared the balancing behaviour of subjects with severe visual impairment (referred to here as blind subjects) to that of a matched group of normal subjects during quiet stance and during dynamic postural tasks. Blind and normal subjects were naïve to the procedures. All subjects performed the trials under both EC and EO conditions. The main finding was that the balancing strategies of the blind subjects were substantially superimposable to those of the normal subjects EC. Thus, there was no evidence for long-term compensation for lack of vision by the increased use of alternative sensory modalities to stabilize body in space.

So far, the literature about the ability of blind people to maintain equilibrium in static postural tasks was limited and non-conclusive. Some studies show that blind subjects can maintain equilibrium better than sighted subjects (Pyykko *et al.*, 1991; Juodžbaliene and Muckus, 2006); other studies show opposite results (Stones and Kozma, 1987; Portfors-Yeomans and Riach, 1995). We found here that body sway was larger with EC than EO in normal subjects, confirming numerous reports in the literature (Schieppati *et al.*, 1999). The blind subjects, regardless of EO or EC, behaved in the same way as normal subjects EC.

Dynamic postural stability, as inferred by the automatic postural responses to impulsive perturbations produced by sudden displacement of the support base, has been recently investigated in blind subjects (Nakata and Yabe, 2001). No differences were found in these simple postural responses between blind and sighted subjects with EC or EO during platform rotations or translations. In our hands, during the complex dynamic task consisting in counteracting the continuous translation of the moving platform, the blind subjects' populations studied in both Pavia and Veruno did not stabilize their head in space like normal subjects, with either EO or EC and regardless of the platform oscillation patterns. The head oscillations followed or even overshot the displacement of the moving platform, seemingly reproducing the behaviour of the normal subjects EC. However, some differences from the balancing behaviour of normal subjects EC were observed. In blind subjects, with both EO and EC and at all translation frequencies, head and hip oscillated, on average, significantly more than in the normal subjects with EC. The other significant difference was that blind subjects, independently of the eyes being open or closed, showed a stronger coupling between the head motion and the platform periodic oscillation, as indicated by the higher values of the cross-correlation between head and foot markers. This was true also for the coupling between head and hip. This might imply that blind subjects would not exploit all body's degrees of freedom. The phenomenon seems to be reminiscent of that previously observed in a group of elderly subjects with EC (Nardone *et al.*, 2000), where the head antero-posterior oscillations and the cross-correlation values between segments' displacements were also larger than in young subjects. In both the elderly and the blind subjects' populations, this behaviour might be related to the presence of increased postural anxiety (Klein *et al.*, 2003; Sibley *et al.*, 2007), in turn leading to a stiffer mechanical linkage between body segments. However, this stronger coupling between head and the platform movement for the blind may be a strategy to increase the vestibular system stimulation and get a stronger gravito-inertial input for balance control (Buchanan and Horak, 2001–2002;

Corna *et al*., 2003). It should also be considered that, when head and trunk move *en-block*, the vestibular input can possibly give a more reliable estimate of the movement of the body's centre of mass. In this light, normal head mobility in blind subjects could blur the balance-effective coding from the labyrinth. An alternative possibility is that there may be relatively more head movement unrelated to platform translation in sighted subjects, whereas there is an acquired relative lack of active, exploratory independent head movement in blind subjects. In the present study, under all circumstances, the time lag between head and malleolus, although varying as a function of platform oscillation patterns, was not different between blind and sighted subjects EC, indicating that the higher CC values or the larger head and hip oscillations, in the blind subjects were not explained by a delay in the coordination between body segments (Schieppati *et al*., 2002).

The role of vision during quiet stance and dynamic equilibrium

In normal subjects, stabilization of the head in space is a strategy to maintain equilibrium, both during natural movements like locomotion (Pozzo *et al*., 1990; Assaiante and Amblard, 1993; Bril and Ledebt, 1998) and complex dynamic equilibrium tasks (Pozzo *et al*., 1995). It seems that vision facilitates this phenomenon (Guitton *et al*., 1986; Pozzo *et al*., 1995; Corna *et al*., 1999; Buchanan and Horak, 1999; Cromwell *et al*., 2002; Buchanan and Horak, 2003; De Nunzio *et al*., 2005), probably because head stability provides both gaze stabilization and a reference for organizing the movement of the other segments. During the continuous movement of the platform, if vision is not available, subjects let the head go and re-reference their balance control on inputs from plantar cutaneous or multiple proprioceptive or labyrinth receptors, all elicited by the moving platform. It has been shown that normal subjects can stabilize the head without vision on the platform, but only by means of a voluntary effort, and more or less successfully depending on the frequency of translation (Buchanan and Horak, 2003).

The limited head oscillation during the balancing behaviour EO confers the key advantage of minimizing the effort for balancing, since inertia is reduced by the diminished velocity of head and trunk and the leg muscle activity is accordingly reduced (Corna *et al*., 1999; Buchanan and Horak, 2001; De Nunzio *et al*., 2007). This EO balancing behaviour in normal subjects is also presumably accompanied by increased perceived stability, since the centre of mass never approaches the limits of stability, thereby diminishing the risk of falling (Schieppati *et al*., 1994; Schieppati *et al*., 2002). In this context, vision seems a means of minimizing the equilibrium destabilization rather than a condition for gaze fixation, since the visual image is not really steady: in fact, the head A–P oscillations are not at all negligible even under EO condition (head SDs with EO are about 60% of EC).

This balancing task has also been previously tested in various patient groups. As expected, somatosensory and vestibular impairment produced larger than normal body oscillations. Overall, however, vision was sufficient to allow the head stabilization strategy in spite of the sensory impairments: the stabilizing effect of vision was independent of peripheral neuropathy or vestibular deficit or basal ganglia diseases (Buchanan and Horak, 2001–2002; Corna *et al*., 2003; Nardone and Schieppati, 2006; Nardone *et al*., 2006). It is reasonable to assume that blind subjects would also crave for minimizing the cost of balancing and the risk of falling. In fact, they do not have the possibility of getting visual information when their body becomes destabilized, as would occur instead in normal subjects who can simply open their eyes if in danger of falling. The question is then whether or not blind subjects do exploit other sensory modalities for reducing the cost of balancing and stabilizing their head and body in space during the platform translations. Among these modalities, the contribution to postural control of cutaneous (plantar pressure sensors, Maurer *et al*., 2006), proprioceptive spindle (Courtine *et al*., 2007) and load receptors (Dietz, 1998) and graviceptive information should be reweighed in blind subjects, particularly under dynamic conditions. Notably, an increased reliance on vestibular information has been shown to occur under critical balancing conditions in normal subjects (Fitzpatrick *et al*., 1994; Welgampola and Colebatch, 2001; Day *et al*., 2002; Peterka, 2002; Cenciarini and Peterka, 2006).

Compensatory or general-loss hypothesis?

Based on the idea that blind people develop capacities of their remaining senses that exceed those of normal subjects, we had supposed that blind subjects would take advantage of their other sensory inputs for controlling balance. This would reduce as much as possible both their energy expenditure and the oscillations of their centre of mass, thanks to a cross-modality plasticity process. The brain does possess the capacity to reorganize itself after peripheral injuries or deprivation, as to enable neighbouring cortical regions to expand into the space normally occupied by input from the deprived sense organs [Vidyasagar, 1978 (rat); Hyvarinen, 1981 (monkey); Rauschecker, 1996 (cat)]. Also, growing experimental evidence suggests that in blind subjects the areas commonly associated with the processing of visual information are active in response to auditory (Kujala *et al*., 1992; Theoret *et al*., 2004) and tactile stimulation (Uhl *et al*., 1993) or during Braille reading (Sadato *et al*., 1996; Cohen *et al*., 1997; Sadato *et al*., 1998; Pascual-Leone *et al*., 2000). Parts of the visual cortex are recruited by other sensory modalities to process sensory information in a compensatory cross-modal manner

(Cohen *et al*., 1997; Theoret *et al*., 2004; Merabet *et al*., 2005; Ptito *et al*., 2005). Our results are at variance with that supposition. If anything, blind subjects performed the trials with larger A–P body displacement than normal subjects with EC, thereby getting closer to their limits of stability. These results were unanticipated and are not consistent with the compensatory hypothesis, at least with a strong version of it. Therefore, no cross-modal plasticity appears to take place and substitute for vision in the ability to stabilize body position with respect to space.

However, the compensatory hypothesis had been advanced on the basis of experimental evidences obtained in specific tactile or auditory tasks. For instance, plastic changes in visual cortex connected with tactile finger perception in Braille readers seem to be driven by the experience with Braille reading, rather than by blindness *per se* (Pascual-Leone and Torres, 1993; Sterr *et al*., 1998; Grant *et al*., 2000). Pure motor or sensory tasks, like non-Braille sensory finger stimulation or finger tapping, do not lead to activation of striate cortex, indicating that the brain can discriminate between finger touching and finger reading (Gizewski *et al*., 2003). If activation of the new functional connections of blind subjects is strongly task-related and training-induced (Buchel, 1998; Gizewski, 2003; Kujala, 2005; Ptito *et al*., 2005), one would suppose that blind subjects had no chance to develop superior postural abilities because they never practiced riding the mobile platform before. However, all normal subjects were also naïve to the task too: this notwithstanding, with vision they promptly stabilized head and trunk from the beginning of the trial.

Therefore, the increased oscillation of the blind subjects with respect to normal subjects EC is in keeping with the general-loss hypothesis, which maintains that vision is fundamental for the calibration of the other senses (Rauschecker, 1995*a*; Pascual-Leone *et al*., 2005), even if it is not necessary for vision to be continuously available during a task performance. It should be noted that when normal subjects closed their eyes, they oscillated less than blind subjects with EC. The ample oscillations of blind subjects might be in part explained by the fact that normal subjects had sustained one or more intermingled EO trials during their sessions. Blind subjects lack the interaction of the visual with the motor experiences that normally leads to calibration of the sensory maps (Held and Hein, 1963; Rauschecker, 1995*b*). Therefore, they had no previous cue of head and trunk stabilization. The fact that the platform oscillations were predictable did not help blind subjects, either.

We are not in the position to state whether the absence of cross-modal plasticity puts blind subjects at risk of falling. In fact, owing to the deliberate use of fairly safe platform translation patterns, the study cannot answer the question of whether is it easier to cause to fall over normal subjects with eyes closed or blind subjects, under the present conditions. In principle, it would be in fact possible that 'functional' plasticity with respect to balancing ability in daily living has occurred in blind people, but that this process would not be necessarily accompanied by any acquired ability to stabilize body position with respect to space. Notably, however, several reports in the literature point to increased risk of falling of blind subjects under more ecological conditions (Legood *et al*., 2002).

Differences between acquired and congenitally blind subjects

The cross-modal reorganization of multimodal areas appears to be not restricted to developmental periods but available, at least to some extent, throughout life (Kaas, 1991). Five days of visual deprivation in normal subjects seem to be sufficient to lead to recruitment of the primary visual cortex for tactile and auditory processing (Pascual-Leone and Hamilton, 2001). But animal research has documented that the compensatory effect is much greater if deprivation occurs early in life (Volgyi *et al*., 1993). Therefore, the possibility that congenitally blind subjects performed the static and dynamic tasks better than acquired blind subjects seemed a possible assumption, but it was not confirmed. The two groups of blind subjects showed comparable behaviours for both visual conditions, both during quiet stance and for all frequencies tested and all amplitudes of platform oscillation.

Conclusion

The findings suggest that the controls of quiet stance and of balancing on the mobile platform are unaffected by the long-term absence of vision. The circuits subserving the stabilizing effect of vision seem to be hard-wired, leading to the conclusion that any tactile, proprioceptive or vestibular function, enhanced by enduring brain plasticity starting early in life, cannot replace normal vision. Conversely, it seems that blind subjects use a behavioural strategy leading to larger body oscillations, possibly a condition for increasing the afferent information from the remaining senses. It is not unlikely, however, that long-term repetition of the mobile platform balancing task could improve the capacity of blind people to properly exploit other sensory inflow in order to compensate for loss of vision. This would possibly open rehabilitation perspectives, also in the light of proven improvement of static and dynamic balance performances by practice with the moving platform in patients with vestibular disorders (Corna *et al*., 2003).

Acknowledgements

This investigation was supported by the grants PRIN 2005 no. 2005059738, FIRB 2001 no. RBNE01FJ4J from the Italian Ministry of Education. J. Tarantola and M.V. Beretta helped with data collection. We thank Dr Rosemary Allpress for English editing of the manuscript.

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