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Goal-directed linear locomotion in normal and labyrinthine-defective subjects

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Abstract When a subject is walking blindfolded straight ahead towards a previously seen target, the brain must update an internal representation with respect to the environment. This study examines whether the information given by the vestibular system is necessary for this simple path integration task and gives a quantitative description of locomotor behaviour during the walk by comparing ten normal and seven bilateral labyrinthine-defective (LD) subjects. Each subject performed 20 blindfolded walks (EC) and ten walks with eyes open (EO) towards a target attached to the floor 4 m in front of them; these walks were made at different velocities. The positions of head, trunk and feet were recorded using a 3D motion analysis system. No significant difference was found between normal and LD groups in terms of the distance error of reaching the target, while LD subjects showed a larger lateral error. Path curvature, expressed as the standard deviation of the angle between the direction of one step and straight ahead, was found to be significantly larger for LD subjects in the EC condition, demonstrating their instability when walking without vision. Mean walking velocity was lower for LD subjects than for normal subjects in both EC and EO conditions. Both groups walked faster with eyes open; LD subjects increased their velocity by increasing step length, normal subjects by increasing step frequency. Head stabilisation in the frontal plane during locomotion was not significantly different between LD and normal subjects, whereas both head and trunk rotation were slightly larger in LD subjects during blindfolded walking. The results show that bilateral LD subjects are able to perform linear goal-directed locomotion towards memorised targets. Thus, the vestibular system does not appear to be necessary for active linear path integration.

Key words Path integration · Locomotion
Vestibular system · Vestibular disorders · Human

Introduction

Goal-directed locomotion requires several capabilities, such as sensing the environment, route planning and the execution of movements. For human navigation, numerous studies focusing on these different faculties have been performed examining various kinds of locomotory tasks, from locomotor pointing (Thomson 1980), i.e. reaching a previously seen target by walking without vision, and reproduction of movements (Klatzky et al. 1990) to complex tasks such as navigation in buildings (Thorndyke and Hayes-Roth 1982).

Even a simple linear locomotory task such as locomotor pointing requires the ability to estimate one's position relative to the environment. When all external cues such as vision, sounds or variations in ground surface are excluded, the only possibility left is the use of knowledge of self-motion to compute an estimate of position relative to earth. This so called "idiothetic" navigation (Mittelstaedt and Mittelstaedt 1973) contributes to the successful homing performance of several kinds of animals, such as spiders (Mittelstaedt 1985), desert ants (Müller and Wehner 1988) and small mammals (Mittelstaedt and Mittelstaedt 1980; Etienne et al. 1985). The required computation consists of integration of motion information and is therefore called "path integration". In mammals, when no visual cues or optic flow are available, self-motion can be derived from the motor commands to the legs, sensed by proprioceptive feedback or computed from acceleration information provided by the vestibular system.

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Since Thomson (1980) first examined the ability to walk blindfolded towards a previously seen target, this task has been of great interest to many authors (Corlett 1986; Elliot 1987; Klatzky et al. 1990; Rieser et al. 1990). In general, normal subjects are quite accurate in reaching a previously seen target over a wide range of distances and also have a good knowledge of self position during the walk, as demonstrated by continuous pointing to a previously seen target (Loomis et al. 1992). However, none of these authors investigated what kind of information is used for path integration without vision.

For the perception of passive linear displacement, the importance of the vestibular sensors has already been shown (Israël and Berthoz 1989) by comparing the performance of normal and bilateral labyrinthine-defective (LD) subjects in reproducing their displacement by appropriate eye movement amplitude. In the case of body rotations, Guedry (1971) demonstrated the ability of subjects to correctly judge their displacement after passive whole body rotations, but a similar task could not be performed correctly by LD subjects (Metcalfe and Gresty 1992). Those results led us to investigate the potential contribution of the vestibular system to distance estimation in active walking which had been proposed by Beritoff (1965) and Potegal (1982), based on experiments in animals and humans.

Comparing errors of distance estimation in active walking and passive transport (Mittelstaedt and Glasauer 1991) at different speeds (overshooting for slow velocities in active walking, undershooting in passive transport) suggests that two different integrative mechanisms must be responsible for the performance. Based on the hypothesis that subjects act on the learned relationship between visual and proprioceptive inputs when walking without vision, Rieser et al. (1988) were able to show significant modifications in distance estimation after changing the normal relationship between visual and proprioceptive flow by pre-experimental training. This is a further hint of the importance of the proprioceptive system.

Worchel (1952), who studied the capabilities of LD subjects in two different return tasks with a triangle route, found no differences between normal and LD subjects, but suggested from his experiments that kinaesthetic cues are very important. In contrast, Beritoff (1965), who compared more qualitatively the spatial abilities of normal and LD children in blindfolded locomotion, stated that the vestibular sense is much more important than proprioception. Possible differences in linear walking were not systematically examined by those authors.

LD subjects walking without vision are not able to maintain stable equilibrium, as shown by Pozzo et al. (1991b). This causes additional problems for non-visual goal-directed locomotion, and which have to be taken into account. Even if non-vestibular self-motion cues are sufficient for linear path integration, a continuous compensation for imbalance-induced disturbances of the planned trajectory – such as short stops or lateral deviations – is required to reach the given target position.

The present study sets out to examine whether the acceleration signals given by the vestibular system are necessary for computing self-position relative to the environment during active linear walking. We give a quantitative description of the locomotion patterns and the performance of reaching a target at different walking speeds in bilateral LD and normal subjects, and compare the results of both groups. A preliminary account of the work has previously been given (Glasauer et al. 1993a, b).

Materials and methods

Subjects and procedure

Ten normal subjects (seven female, three male; aged 20–45 years) and seven bilateral LD subjects (six female, one male; aged 26, 26, 40, 45, 50, 59 and 68 years) participated in the study. Some of them wore spectacles; all could see the target without difficulty. None of them had experience in performing the experiment. Six LD subjects had bilateral caloric areflexia, due to ischaemia (2), gentamicin (3), streptomycin (1) and Cogan syndrome (1); one LD subject had bilateral section of the eighth cranial nerve after otoneurosurgery for bilateral acoustic neuroma due to Recklinghausen syndrome. The patients underwent clinical testing of vestibular function (ENT Department, Hôpital Lariboisière, Paris) with the following methods: audiometry, caloric test, eye-head coordination and gaze stabilisation in the frontal plane (Freyss et al. 1989). None of the patients responded to the clinical vestibular tests. However, total destruction of vestibular function was assured only for the neuroma patient, due to the bilateral nerve section. Imaging (CT and MRI) was performed in order to rule out lesions of brain and/or posterior fossa. The neuroma patient had brain lesions due to surgery and a section of the right optic nerve. However, neurological examination showed no proprioceptive disorders and, as documented below, his results in our experiment exhibited no significant differences from those of the other LD subjects. The Cogan syndrome patient had been subject to disorders for 2 years, whereas the disorders of all the others had appeared more than 10 years before the study. All the patients had undergone vestibular rehabilitation treatment (A. Semont) and, except for the Cogan syndrome subject, were tested at the end of rehabilitation.

One of the LD subjects (gentamicin, age 68 years) was excluded from the analysis of distance and lateral error, because she made no serious attempt to solve the task. However, her walking pattern (step characteristics, head and trunk rotation) showed no significant differences from that of the other LD subjects and was consequently included for the final analysis.

The subjects were asked to walk unguided and blindfolded to a previously seen target at five different self-paced velocities. The target consisted of a white cross (20 × 20 cm) located on the otherwise dark ground 4 m in front of them (see Fig. 1). In addition, they were requested to close their eyes during the task. To exclude auditory cues, subjects were equipped with earphones and listened to white noise from a portable tape recorder. Before starting their walk, the subjects were told which speed range (very slow, slow, normal, fast, very fast, presented in pseudo-random order) they had to use. They were free to choose their own velocity ranges. The subjects started after their blindfold had been seured and they had counted to three, thus indicating that the experimenter should start data acquisition. During the blindfolded walks, one of the experimenters walked behind the subject to prevent them from falling. The subjects stopped when they thought they had reached the target position. After the walk was completed, the experi-

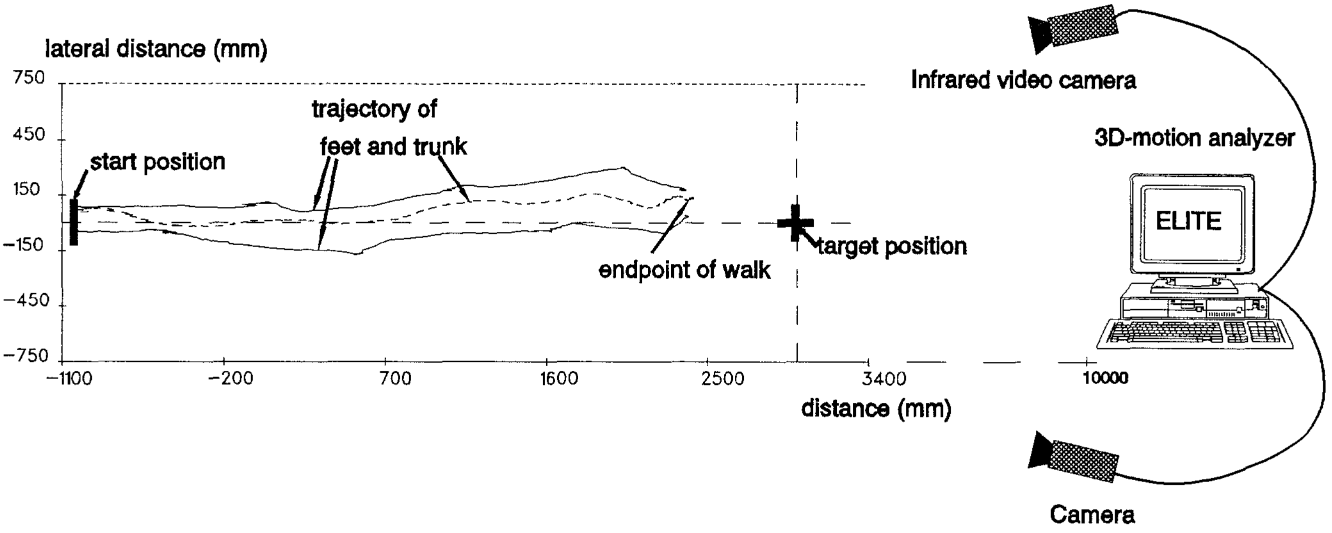

Fig. 1 Overhead view of the experimental setup with an example of the trajectories of feet and trunk during one walk. The trajectories are computed by the ELITE 3D-motion analyser from the positions of infrared reflecting markers attached to the subject's body. *Abscissa* distance in start-target direction (mm), *ordinate* lateral distance (mm)

menter guided them a few metres further on a curved path, to exclude any feedback information about their performance. They then opened their eyes and walked back to the starting position. Each subject performed four walks with closed eyes (EC) and two walks with open eyes (EO) for each of the five walking speeds, in order to compare locomotion in both cases.

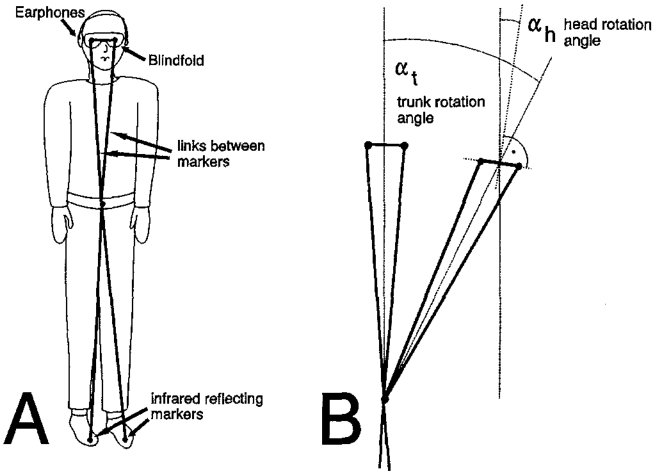

Fig. 2 **A** Positions of the five infrared reflecting markers attached to the body of the subject. **B** Head rotation angle α_h and trunk rotation angle α_t in the frontal plane as computed from the marker positions of the head and trunk with respect to gravity. Angles are projected onto a frontoparallel plane

Data acquisition and analysis

The 3D spatial position of the head, trunk and feet of the subjects was recorded by an ELITE, infrared-video, motion analyser. Two infrared-reflecting markers were attached to the blindfold (marker distance 8.5 cm) to give the position of the head; one at the tip of each foot and one at the trunk between the hips approximately at the navel (see Fig. 2). Two cameras (distance between cameras 2.5 m), positioned 10 m in front of the starting position at 1.7 m above ground level, recorded marker locations with a rate of 100 images per second. The ELITE software determined the three-dimensional spatial position of each marker from the two camera images for further analysis. Automatic software (interactively controlled) detected steps to investigate the locomotion pattern as well as the beginning and end of the movement. One step was considered to be finished when both foot markers had the same longitudinal position along the path, i.e. when one foot passed the other (see bottom Fig. 3). The start of the movement was detected when one foot left ground level and the end when both feet remained stationary on the floor for the rest of the acquisition.

The measurement noise perturbing the marker acquisition was evaluated by averaging the positions of one static marker at the starting site and one at the target site for 1 s. The mean standard deviation of the marker coordinates was largest for the longitudinal direction (start 5.27 mm; target 1.07 mm) and lowest for the lateral direction (start 0.45 mm; target 0.16 mm).

Several parameters of locomotion (step length and frequency, head and trunk rotation, step direction), which are described in the following section, were computed in this primary analysis. The data used to evaluate head and trunk rotation angles were filtered by a gaussian low-pass filter (cut-off frequency 10 Hz, i.e. attenuation of 45.6% at 10 Hz) to reduce the influence of the measurement noise on the standard deviation of these measures. In the secondary, statistical analysis, the means of those parameters were compared by Student's *t*-test or the *F*-test. To compute and compare means of correlation coefficients Fisher's *z*-transformation was used to improve normality. Means of coefficients are given after transformation back to the original scale.

Mean step length and frequency were evaluated excluding the last step of every walk, which was often a correction step smaller than the others (see Results). In the case of missing values, for example hidden foot markers, the respective parameters were not computed for all steps or times. Due to constraints of the ELITE system (an early version permitted acquisitions up to 10 s) on a small number of trials (nine trials in the EC condition from three different subjects), the final position of the walk could not be determined. For some trials, when the subject overshot the target by more than 1.2 m, the final position of the walk had to be determined from the trunk position and not, as usual, from the foot markers.

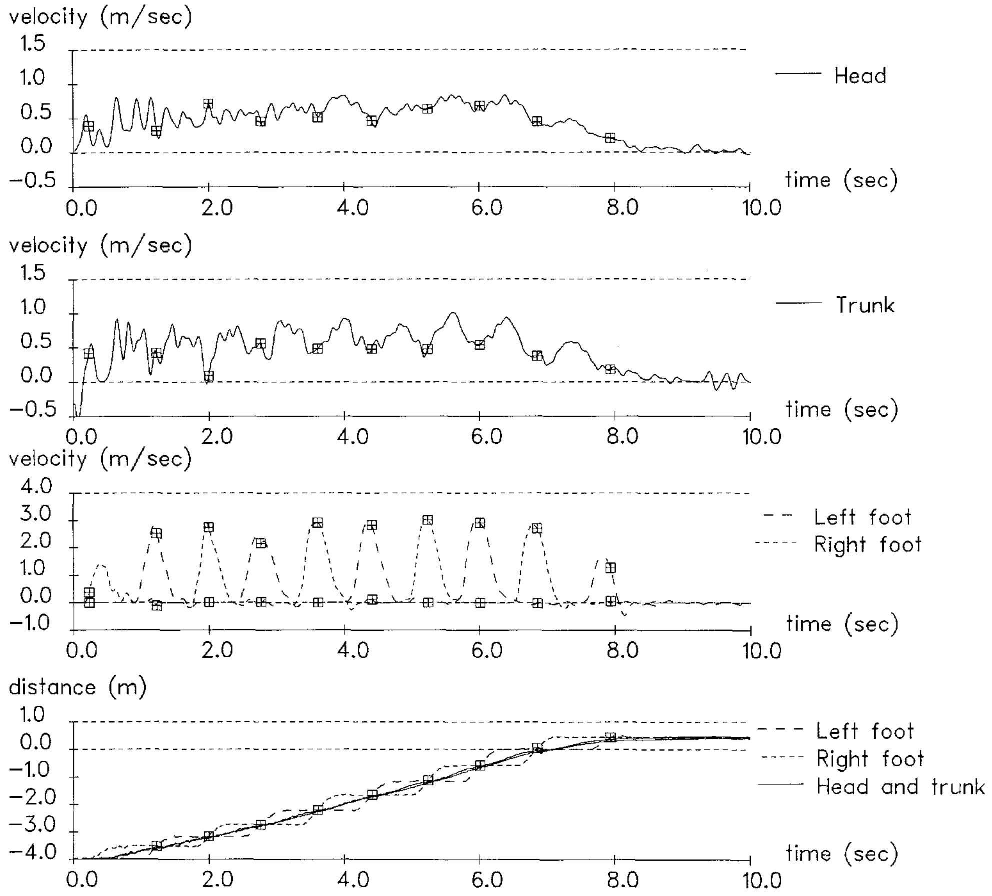

Fig. 3 Example of the linear velocity of feet, trunk and head along the walking direction (*upper parts* ordinate, velocity in m/s) and the respective positions of head, trunk and feet markers (*lower part* ordinate, distance walked in m) plotted over time (s). *Small squares* depict the start or end of one step, determined when one foot passes the other (*lower part*). Target position (*dashed line, lower part*) is at 0. In this example, trunk velocity varies more than head velocity

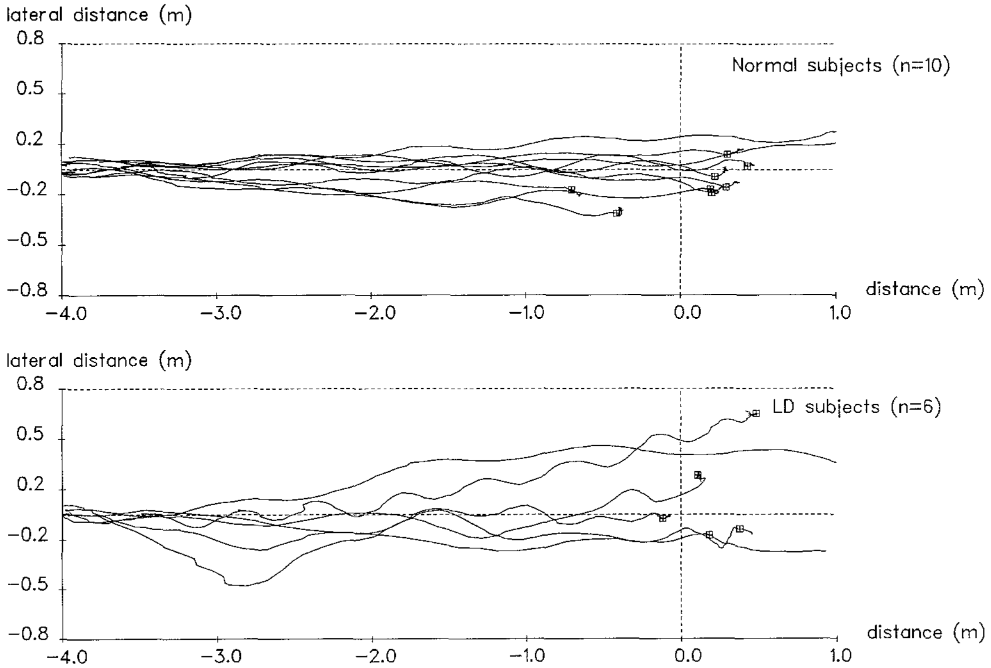

Fig. 4 Examples of walking trajectories (trunk marker): the 10th walk (eyes closed, "slow" walk) for all subjects plotted as on overhead view (*Abscissa* distance in start-target direction in m, *ordinate* lateral distance in m, target position at 0). *Upper part* normal subjects, *lower part* LD subjects. *Squares* indicate final positions of the walk. Some of the subjects overshot the target by more than 1 m in this condition

Results

As an example of raw data, Fig. 4 shows the trajectories of the trunk marker and the final endpoints of the walk, in an overhead view, with identically scaled axes. The trajectories are plotted for all subjects for a "slow" walk in the eyes closed (EC) condition. Note that some of the subjects overshot by more than 1 m (endpoints not drawn) and that the normal subjects and LD subjects obviously differed with respect to the curvature of the trajectories, the latter deviating up to nearly 50 cm from the desired straight start-target direction. Nevertheless, some of them could compensate during their walk for the lateral deviation, which was often caused by unstable equilibrium, and returned close to the ideal straight path.

One illustrative example of the linear velocity of head, trunk and feet along the walking direction [EC condition, normal subjects, computed from the gaussian low-pass filtered (10 Hz) positions of the markers] is given in Fig. 3. The lowest part of the figure shows the respective positions of head and feet (see Pailhous and Bonnard 1992). Head velocity, almost constant during the walk, decreases a few steps before the final position (see step marks), suggesting that the movement has been planned in advance, at least for this period of time. Furthermore, the last step is generally shorter ("corrective" step, see statistical analysis below), as found by Laurent and Thomson (1988) for the same task. This suggests that the path is not computed as a function of the number of steps, but rather that it is represented as a distance relative to the target position measured in units shorter than step length.

In the following analysis, the different parameters of performance and locomotion are described and compared for both groups and conditions. Because the Cogan syndrome patient had not yet completed vestibular rehabilitation, the significance levels for all comparisons between groups and conditions have been computed with and without this subject. The same was done for the neuroma patient. Though no important differences were found, significance levels changed from slightly below 5% to slightly above 5% in some cases described below.

Performance

The endpoints of all walks in the EC condition and the respective 95% confidence ellipses for each subject relative to the target position are shown in Fig. 5. In general, both normal subjects (0.162 ± 0.369 m) and LD subjects (0.388 ± 0.356 m) slightly overshot the target and had larger longitudinal than lateral deviations (absolute lateral error: normal, 0.071 ± 0.060 m; LD, 0.216 ± 0.074 m). Distance errors did not differ statistically for either groups (*t*-test, Table 3). This is true even if computed without the Cogan syndrome patient, who was the only LD subject undershooting the target. The neuroma patient also overshot the target (0.533 ± 0.453 m), but was not the subject with the largest error.

Variation of the individual end point distributions of the LD subjects was larger, as revealed by the larger variable error (mean standard deviation) of the final distance error (normal, 0.322 ± 0.072 m; LD, 0.449 ± 0.129 m; $P < 0.023$, *t*-test). This difference indicates that LD subjects did not walk towards the target position on repeated trials with the same accuracy as normal subjects.

A computation of the mean lateral signed errors would depend mainly on the individual left-right preferences of the subjects, but could not assess the lateral error from target position. Thus we evaluated a measure for absolute lateral errors. The absolute lateral error itself is not normally distributed and therefore cannot be compared between groups by standard methods. Instead, the root-mean-squared (rms) lateral error is computed, which can be compared by means of the *F*-test under the justifiable assumption that the mean lateral error over all subjects should be zero. This parameter was significantly different between normal and LD subjects (*F*-test, Table 3), showing that the lateral distribution of endpoints is more widespread for the group of LD subjects.

Neither velocity [as found by Mittelstaedt and Glasauer (1991) for individual subjects] nor any of the following parameters were correlated significantly with distance or lateral errors, indicating that the performance was not influenced significantly by the parameters examined below.

Walking trajectory

In order to provide a measure of the curvature of the walking trajectory, the standard deviation σ_s of the angle α_s between the start-target direction and the direction of each step was computed (see Fig. 6). Step direction is given as the direction between start and end position of one step. Given a straight trajectory of each foot, σ_s would be 0° independently of the walking direction.

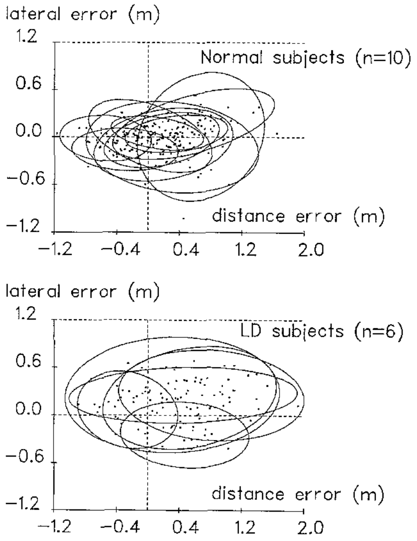

Fig. 5 Final endpoints of all walks (*small dots*) and 95% confidence ellipses for each subject relative to target position for LD subjects (*lower part*) and normal subjects (*upper part*) in the eyes-closed condition. The centre of an ellipse gives the mean endpoint of one subject; 95% of the estimated normal distribution of endpoints lies within the ellipse. *Abscissa* distance error (equivalent to distance from target) in m, *ordinate* lateral error (equivalent to lateral deviation from the start-target direction) in m

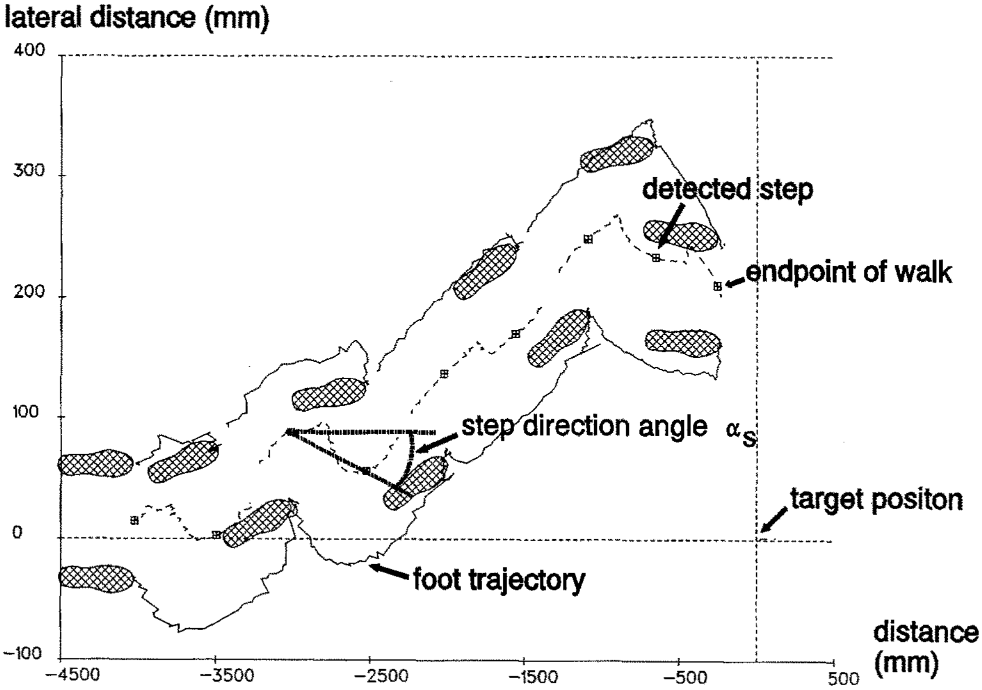

Fig. 6 Computation of the step angle α_s as the angle between the direction straight ahead and the direction of one step. Note the different scaling of the axes (*abscissa* distance in start-target direction in mm, *ordinate* lateral distance in mm). *Small squares* indicate start or end of one step detected when both feet markers had the same position in the direction of walking (see also Fig. 3, lower part)

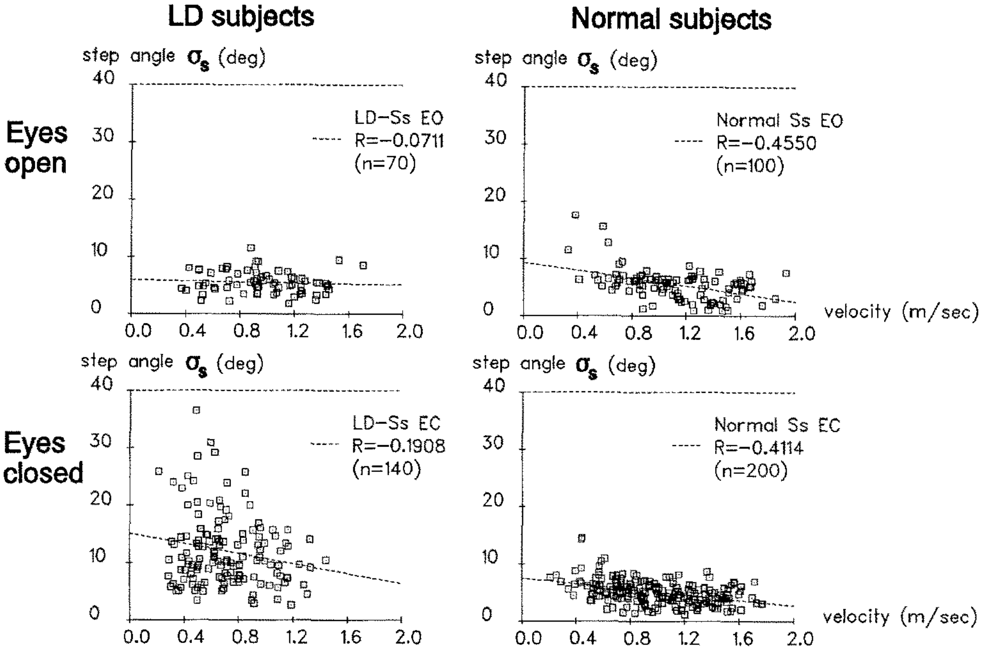

Fig. 7 Standard deviation of step angles σ_s (in deg) with respect to the direction straight ahead for LD and normal subjects in both eyes-open and eyes-closed conditions plotted over mean walking velocity (in m/s). Correlation lines are *dashed*, the correlation coefficients are indicated as *R*, and *n* gives the number of walks performed by each group in each condition

In Fig. 7, σ_s is plotted versus mean walking velocity. σ_s is, as standard deviation, not exactly normally distributed. However, a more adequate analysis based on a *F*-test comparison of the chi-square distributed step angle variances did not yield significance values qualitatively different from those described below.

For normal subjects, σ_s was not different between EC (5.07±1.32 deg) and EO (5.42±2.13 deg) conditions (Table 1), but did depend significantly ($P<0.001$, see Fig. 7) on walking speed. The path curvature index σ_s decreased with increasing velocity, confirming the qualitative observation of straighter walks for faster speeds. The difference between EC (11.92±2.22 deg) and EO (5.51±1.06 deg) conditions for LD subjects (Table 2) and also between normals and LD subjects in the EC condition (Table 3) was highly significant, mirroring the equilibrium problems of LD subjects in a blindfolded walk. In contrast to normal subjects, path curvature of LD subjects did not depend significantly on walking speed (Fig. 7). For the EC condition, the smallest σ_s of the LD subjects was still larger than the largest σ_s of the normal subjects. Moreover, the comparisons of each LD

Table 1 Differences between walking with eyes closed and eyes open in ten normal subjects (t-test; n.s. denotes significance values above 5%). Note that normal subjects made faster steps in the EO condition to establish a faster mean walking velocity

Parameter	Eyes closed	Eyes open	Significance
Mean velocity (m/s)	0.986±0.118	1.128±0.151	$P<0.030$
Step frequency (per second)	1.615±0.093	1.728±0.099	$P<0.017$
Step length (m)	0.659±0.085	0.708±0.079	$P<0.197$ n.s.
Variability σ_s of step direction (deg)	5.07 ±1.32	5.42 ±2.13	$P<0.663$ n.s.
Variability σ_h of head rotation (deg)	1.50 ±0.48	1.67 ±0.52	$P<0.435$ n.s.
Variability σ_t of trunk rotation (deg)	1.94 ±0.57	2.14 ±0.55	$P<0.432$ n.s.

Table 2 Differences between walking with eyes closed and eyes open in seven LD subjects (t-test; n.s. denotes significance values above 5%). In contrast to normal subjects, LD subjects took longer steps to walk faster in the EO condition. Note the difference in σ_s between conditions, indicating much larger path curvature in the EC condition

Parameter	Eyes closed	Eyes open	Significance
Mean velocity (m/s)	0.713±0.127	0.972±0.114	$P<0.002$
Step frequency (per second)	1.714±0.110	1.664±0.130	$P<0.460$ n.s.
Step length (m)	0.464±0.082	0.625±0.052	$P<0.0009$
Variability σ_s of step direction (deg)	11.92 ±2.22	5.51 ±1.06	$P<0.00001$
Variability σ_h of head rotation (deg)	1.97 ±0.51	1.46 ±0.39	$P<0.064$ n.s.
Variability σ_t of trunk rotation (deg)	2.73 ±0.86	1.80 ±0.62	$P<0.037$

Table 3 Differences between walking in seven LD (for distance and lateral error six LD) and ten normal subjects for the EC condition (t-test, except F-test for root-mean-squared lateral error; n.s. denotes significance values above 5%). Lateral and variable distance error, but not constant distance error, are greater for LD subjects, as is path curvature, indicated by σ_s. Slower velocity of LD subjects than of normal subjects is caused by shorter mean step length

Parameter	LD subjects	Normal subjects	Significance
Distance error (m)	0.388±0.356	0.162±0.369	$P<0.251$ n.s.
Variable distance error (m)	0.449±0.129	0.322±0.072	$P<0.023$
Root-mean-squared lateral error (m)	0.227	0.091	$P<0.019$
Mean velocity (m/s)	0.713±0.127	0.986±0.118	$P<0.0004$
Step length (m)	0.464±0.083	0.659±0.085	$P<0.0003$
Step frequency (per second)	1.714±0.110	1.615±0.093	$P<0.062$ n.s.
Variability σ_s of step direction (deg)	11.92 ±2.22	5.07 ±1.32	$P<0.00001$
Variability σ_h of head rotation (deg)	1.97 ±0.51	1.50 ±0.48	$P<0.071$ n.s.
Variability σ_t of trunk rotation (deg)	2.74 ±0.86	1.94 ±0.57	$P<0.036$

subject with the mean σ_s of normal subjects (EC) were significant ($P<0.01$). This parameter might therefore serve as an indicator to discriminate between normal and LD subjects.

Locomotor patterns and velocity

Mean walking velocity in the EO condition was significantly higher than for EC in both groups (see Table 1, Table 2) and, in both conditions, higher for normal than for LD subjects. This confirms two qualitative observations: in the EC condition, LD subjects sometimes had to stop for a short time to recover their balance, and they felt unsafe when walking fast and thus chose slower velocities than normal subjects.

To assess whether subjects were able to keep to the velocity ranges requested by the experimenter, measured walking velocities were compared to the required velocity ranges. Normal subjects varied up to ±1 range and LD subjects up to ±2 ranges from the required velocity. However, in most walks, the desired velocity range was chosen (LD EC 73.6%, LD EO 81.4%, normal EC 85.0%, normal EO 80.0%). Some of the erroneous walks might have been due to misunderstandings about the required velocity, whereas some others are related to stops during walking due to equilibrium problems, as mentioned above, leading to slower mean velocities than required.

Mean step length and frequency were computed for every walk. Mean step length and mean step frequency both increased with increasing walking velocity (see Fig. 8). Both parameters were highly significantly related to walking velocity (length versus velocity, $r>0.87$; frequency versus velocity, $r>0.91$ except LD EC $r=0.65$). For LD subjects, the correlation between step length and step frequency in the EC condition was not as high as that for normal subjects, as indicated by the

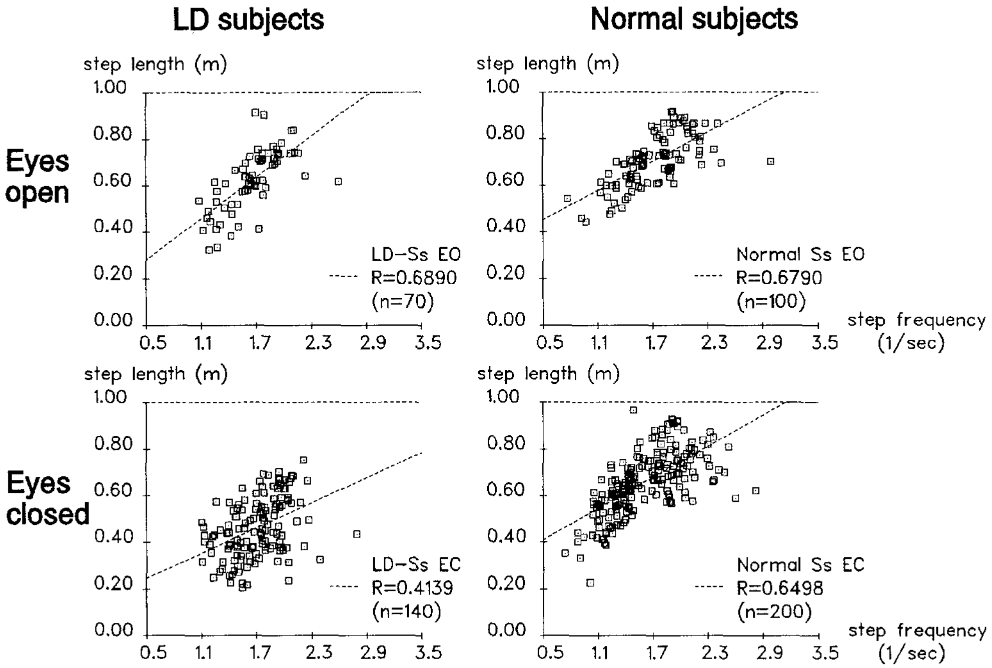

Fig. 8 The relationship between step length (*ordinate*, in metres) and frequency (*abscissa* in steps per second) for all subjects and conditions. Correlation coefficients are indicated by *R*, and *n* gives the number of walks performed by each group in each condition. Correlation is weakest for the eyes-closed walks of the LD subjects

correlation coefficients (normal, $r = 0.65$; LD, $r = 0.41$; see Fig. 8). Again, this was caused by their unstable walks.

The correlations between mean step length and mean step frequency were also evaluated separately for all subjects in both conditions. The means of the correlation coefficients differed significantly from 0 for both groups (LD subjects $P < 0.001$; normal subjects: $P < 0.00001$ with a *t*-test). As indicated by the significance levels, the mean correlation coefficient was weaker for LD subjects (EC 0.701, EO 0.935) than for normal subjects (EC 0.908, EO 0.941), especially in the EC condition. The fact that the average of individual correlation coefficients was much higher for all groups and conditions than the coefficients of a correlation of the pooled data (shown in Fig. 8) indicates that the relation between step frequency and step length differed among individuals.

Normal subjects made faster, but not longer steps in the EO condition (Table 1). In general, LD subjects made shorter steps than normal subjects (Table 3), but mean step frequency was not different. Similarly, step frequency was the same for LD subjects in EC and EO; in contrast to normal subjects, their faster mean velocity in EO was caused by larger steps (Table 2).

A comparison of the length of the last step to the target with the mean of all other steps showed that the last step was significantly shorter ($P < 0.0015$, *t*-test) than the others. This corrective step was found for both groups and both conditions (normal EC: last step 0.389 ± 0.068 m, mean 0.659 ± 0.085 m; normal EO: last step 0.543 ± 0.085 m, mean 0.708 ± 0.079 m; LD EC: last step 0.233 ± 0.113 m, mean 0.475 ± 0.088 m; LD EO: last step 0.446 ± 0.102 m; mean 0.625 ± 0.052 m). Thus, both in the EO and in the EC condition, where no visual feedback can give an estimation of distance, the self-position with respect to the target must have been computed in units smaller than mean step length.

Head stabilisation and head-trunk coordination

To evaluate the stability of the head position in space, the standard deviation σ_h of the head angle α_h in the frontoparallel plane was computed. This parameter, a measure of lateral head rotation, is increased either by head movements in the roll direction or by whole body roll movements without head stabilisation, but does not depend on absolute head position. The standard deviation σ_t of the angle α_t between the head-trunk direction and the vertical projected onto a frontoparallel plane (see Fig. 2) was used as a measure of trunk rotation. σ_t can be interpreted as an index of balance stability. It is independent of stationary shifts between head and trunk markers due to interindividually different marker placement. If a subject were tumbling during his walk, σ_t would increase because of the oscillating movement of the trunk. Both parameters have already been used by Pozzo et al. (1992) to characterise head stabilisation in the frontal plane in normal subjects during more complex equilibrium tasks (balancing on a beam or on a rocking platform).

Figure 9 shows both head and trunk rotation angles for one walk of an LD and a normal subject. The LD subject had an equilibrium disturbance in the middle of the walk which can be seen as a large lateral deviation of the feet. Note the similar head and trunk rotation for the LD subject, which are less correlated for the normal subject.

For LD, but not for normal subjects, mean head ro-

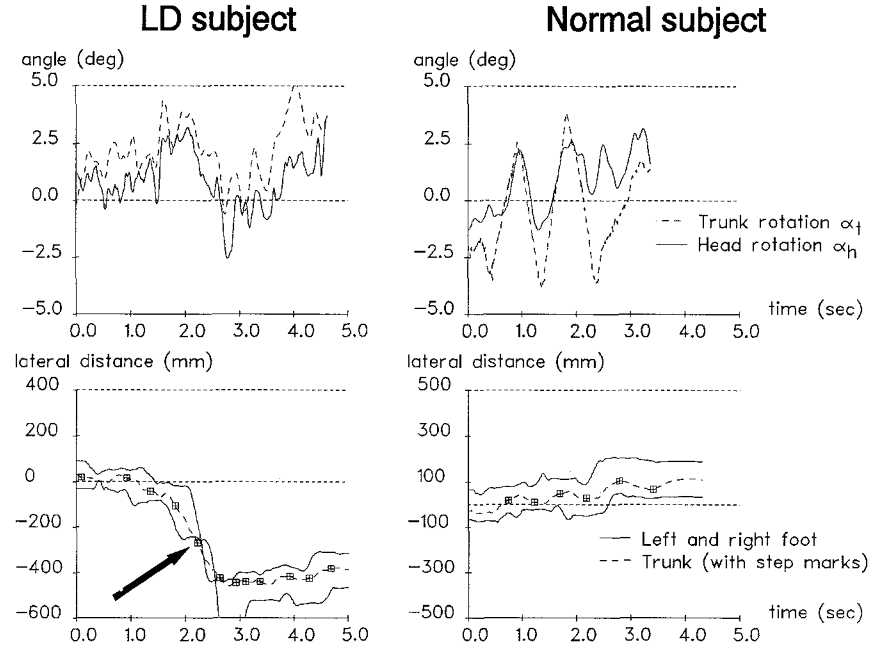

Fig. 9 Head and trunk rotation angles α_h and α_t in the frontal plane (*upper parts*, in degrees) and lateral deviation of the feet and the trunk (lower parts, in metres) for one walk of a normal subject (*right*) and a LD subject (*left*) with eyes closed plotted over time (in seconds). *Small squares* mark the start or end of one step. Head rotation (*solid line*) of the normal subject had in this case a smaller amplitude than trunk rotation (*dashed line*). The LD subject had an imbalance episode in the middle of the walk (indicated by an *arrow*) resulting in a lateral deviation of the trajectory

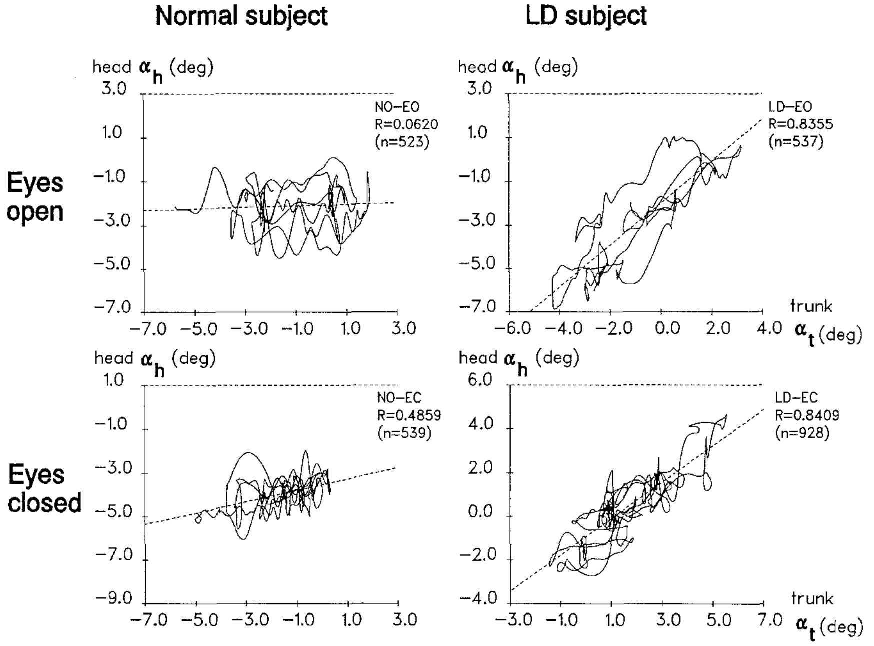

Fig. 10 head rotation angle α_h (in degrees) in the frontal plane plotted over trunk rotation angle α_t (in degrees) for a slow walk for one normal and one LD subject for both EC and EO conditions. Axes are equally scaled. *Dashed line* is linear regression between both parameters (*R* correlation coefficient, *n* number of samples). In this example the normal subject showed good head stabilisation for EC and even better for EO, whereas the LD subject was not able to stabilise his head with respect to earth indicated by the slope being close to one. Note that the absolute angular values depend on the position of the markers on the subject's body and therefore have no significance

tation was slightly larger ($P<0.064$; see Table 2) in the EC condition (1.97 ± 0.51 deg) than for EO (1.46 ± 0.39 deg). The trunk rotation was significantly larger with EC ($P<0.037$; EC 2.73 ± 0.86 deg, EO 1.80 ± 0.62 deg). Comparing LD subjects without the Cogan syndrome patient changed the significance level slightly (head $P<0.097$, trunk $P<0.053$), as did comparison without the neuroma patient (head $P<0.028$, trunk $P<0.042$).

The difference between LD and normal subjects in the EC condition (head 1.50 ± 0.48; trunk 1.94 ± 0.57) was significant for trunk rotation ($P<0.036$, without the Cogan syndrome patient $P<0.023$, without the neuroma patient $P<0.069$). The greater value of the LD subjects confirmed again their unstable blindfolded walk. The value of trunk rotation of LD subjects in the EO condition was smaller than that of normal subjects (head 1.67 ± 0.53 deg, trunk 2.14 ± 0.55 deg), but the difference was not significant. In all cases, head rotation was less than trunk rotation, but the differences were significant neither for normal nor for LD subjects. Likewise, the mean head rotation difference between normal and LD subjects was not significant ($P>0.07$, see Table 3), but the value was larger for LD subjects.

The pure head rotation value σ_h cannot indicate head stabilisation, as a low σ_h could also be caused by a minor trunk rotation. Thus, to evaluate the amount of head stabilisation with respect to the trunk, we computed the linear regression between trunk and head rotation angles α_t and α_h for each walk. The slope of this regression and also the correlation coefficient would be 0 for perfect compensation of trunk rotation and 1 if the head, fixed to the trunk, rotated in the same way as the trunk without any compensation. Evaluation of the regression slope gives a measure of the gain of head versus trunk rotation, as this slope is the covariance between head and trunk divided by the variance of the trunk rotation. Thus, the slope accounts for the assumed dependence or phase relationship of head rotation on trunk rotation and is not merely the ratio between two amplitudes, as is the case with the gain computed from the amplitude spectra.

Figure 10 shows an example of head rotation α_h plotted over trunk rotation α_t for a normal and an LD subject for both EO and EC conditions. In this example, the normal subject could compensate very well for trunk rotation, whereas the LD subject was not able to stabilise his head, which followed the trunk movement almost exactly.

However, a comparison of the mean slopes over groups and conditions revealed no significant differences at all (normals: EC 0.43 ± 0.22, EO 0.48 ± 0.28; LD subjects: EC 0.57 ± 0.21, EO 0.54 ± 0.19). Some of the LD subjects could successfully stabilise their head in space during blindfolded walking, although some of the normal subjects showed quite poor head stabilisation. Five LD subjects and five normal subjects had mean regression slopes larger than 0.5. Two LD subjects had worse stabilisation than the neuroma patient (slope 0.69) and the Cogan syndrome patient (slope 0.65), who was the subject tested most recently after onset of vestibular disorder. Moreover, comparison of the regression slope of single subjects between EC and EO showed significantly better head stabilisation with EO only for one LD and one normal subject.

Discussion

Performance

Distance error and its standard deviation, obtained for the performances of the normal subjects, closely matched those found in the literature. For example, Elliot (1987) reported constant errors in distance of about 0.1 m (overshoot) for reaching a 4 m target (0.16 m in our study) and variable errors of about 0.26 m. Also, Rieser et al. (1988, 1990) stated that the variable error is about 8% of the distance (0.32 m in our study). However, other authors (e.g. Laurent and Thomson 1988) reported undershooting of more than 5%, which probably depended on their different experimental conditions, whereby their subjects were forced to put first a previously assigned foot onto the target. Also in their case (start-target distance 9 m) the target "was only a few metres from a wall", possibly provoking, as suggested by the authors, a "play-safe" strategy. Because in our experiment the distance from the target to the wall exceeded the distance to the target, subjects did not have to fear walking too far.

No significant difference was found between normal and LD subjects for the distance error of walking blindfolded towards the previously seen target. The variable distance error was larger for LD subjects, showing less consistent performance from trial to trial. The lateral deviations, or veering tendencies, showed individual left-right preferences which were more pronounced for LD subjects and which turned out to be significantly different for both groups. Comparison of different locomotion parameters between the EO and EC conditions, and also between normal and LD subjects, suggest that this difference is either due to the equilibrium problems of the LD subjects or to their impaired ability to maintain a direction straight ahead, due to the lack of semicircular canal information. However, it seemed that, most of the time, LD subjects started their walk correctly and then experienced an imbalance episode in between which they could not perfectly correct. This suggests that the imbalance, rather than the inability to walk straight ahead, causes the lateral deviations. However, to differentiate between these two possibilities, experiments involving body rotations need to be performed.

A relationship between walking velocity and distance error similar to the one reported by Mittelstaedt and Glasauer (1991) was not found in this study. As this relationship was obvious mainly for very slow active walks, its absence in our study could be explained by the higher velocity chosen by our subjects for the slow walks. Besides, such a correlation might become significant only for a larger number of walks.

Walking trajectory

The most significantly different parameter between LD and normal subjects in the eyes-closed condition was the path curvature index σ_s, which expresses the variability of the step direction angle. Whereas it had the same value for the LD subjects and the normal subjects when walking with open eyes, the step direction angle of LD subjects varied significantly with closed eyes. The mean of σ_s of LD subjects with EC was more than two times higher than for normal subjects (LD 11.92 ± 2.22 deg; normals 5.07 ± 1.32 deg) or when walking with EO. Because the lowest σ_s of the LD subjects in the EO condition was still higher than the highest one of the normal subjects, the variability of step direction σ_s could perhaps serve as an indicator for labyrinthine deficiency.

Locomotion patterns and velocity

The difference in mean walking speed between EC and EO, which was much more pronounced in LD subjects than in normal subjects, showed the (verbally reported) uncertainty of LD subjects when walking without vision. The difference in velocity of the LD subjects was achieved by shorter step length, a strategy by which they probably tried to avoid balance problems in the EC condition. Ferrandez et al. (1990) found that both young and elderly subjects (over 65 years) – the latter walking more slowly in general – adopt slow velocities in the same way by taking shorter steps. They stated that decreased velocity may ensure safety while walking. However, our normal subjects decreased their velocity during blindfolded locomotion by decreasing step frequency more than step length. This indicates different locomotion strategies among normal and LD subjects when no visual input is available.

The average last step of the walks (both with and without vision) was found to be shorter than the mean of all other steps, thus confirming results of Laurent and Thomson (1988), who reported that subjects change their step length in the three last steps as a fine adjustment for reaching the target position. In their study, the length of the last step was greater without vision, whereas this depended on the absolute distance to the target when walking with vision. The authors claimed than their findings provided evidence for a more "visual" form of representation of target position, such as that suggested earlier by Thomson (1983). The different result we obtained, whereby the last step was always shorter than the preceding ones, can be explained by the difference in paradigms: Laurent and Thomson (1988) required their subjects to finish the walk by placing a previously determined foot exactly onto the target, whereas in our case the foot first touching the target was not specified.

The clear correlation between spontaneously chosen step length, step frequency and walking velocity is conducive to what has been found in the literature (e.g. Grieve and Gear 1966; Nilsson and Thorstensson 1987). This correlation became even clearer in the analysis of individual subjects. Such a fixed relationship between stride length and duration when changing velocity could result from controlling locomotion under normal conditions by a single parameter, as simulated, for example, by Taga et al. (1991) using a theoretical model of a bipedal musculo-skeletal system. This model, the main part of which is a neural rhythm generator receiving proprioceptive and somatosensory feedback, is controlled only by one parameter related to walking velocity and can maintain stable walking or running, even if there are surface changes or mechanical perturbation. Thus, in their model, a reduction of the degrees of freedom is achieved during varying walking velocity, whereas the specific relationship between step length and frequency is determined by the intrinsic structure of the system.

The tight relationship between walking velocity and step length and frequency suggests that one or both of these parameters could be used to acquire the self-motion information necessary to update self-position in space. Mittelstaedt and Glasauer (1993) proposed such a spatial (step length) or temporal (step frequency) path integration of locomotion parameters following experiments in which subjects were asked to dissociate the normal relationship of those parameters, e.g. by walking with small but very fast steps to a previously seen target. Their results suggest that some subjects used step length to determine self-position, whereas others relied on step frequency as a measure of self-motion.

Head stabilisation and head-trunk coordination

Head stabilisation of normal subjects in the frontal plane did not depend on vision, thus confirming the findings of Pozzo et al. (1992) for head stabilisation in the frontal planes during more complex tasks like balancing on a beam. Berthoz and Pozzo (1988) and Pozzo et al. (1991a) found similar results for head stabilisation in the sagittal plane during a blindfolded walk. They suggested that normal subjects could compensate for oscillations of the trunk, probably by using their vestibular system to stabilise the head in space.

Our LD subjects showed a slightly larger head rotation in the frontal plane than normal subjects during blindfolded walking. In addition, their trunk rotation was larger. LD subjects had smaller head rotation with vision, probably because their trunk rotation in this condition was less than for normal subjects. Perhaps LD subjects used a special strategy to avoid balance and head stabilisation problems by simply minimising lateral trunk movements. This would be consistent with the findings of Pozzo et al. (1991a, 1991b) for head stabilisation in the sagittal plane; they found that LD subjects showed smaller up-down head translations than normal subjects and could therefore better stabilise the head. As they suggested, these strategies can help to overcome missing vestibulo-ocular reflexes, thereby avoiding oscillopsia caused by unpredictable head movements during walking (Grossman and Leigh 1990).

Increased head rotation in the frontal plane during blindfolded walking of one LD subject was reported by Miyata et al. (1989). In our study, differences in head rotation between groups were not significant either for eyes closed or eyes open. Only trunk rotation was found to be greater in the blindfolded walks of the LD subjects than in normal subjects, again caused by their equilibrium problems. All patients performed the experiments at least 10 years after onset of vestibular disorder, except for the Cogan syndrome patient who was tested only 2 years after. However, three of the well-compensated LD subjects showed less head stabilisation during blindfolded locomotion than this subject, suggesting that the time of rehabilitation is not the main factor in the ability to stabilise the head in the frontal plane.

Head stabilisation in the frontal plane during passive unpredictable whole body oscillations (max ± 10 deg) has been shown to depend on its necessity due to a visual task such as reading (Gresty and Bronstein 1992).

As these authors noted, they found that good head stabilisation (50%–70% average amplitude gain) during reading helps to overcome the poor torsional vestibulo-ocular reflex (gain 50–70%). Among our subjects, we found no difference in head stabilisation between the EO and EC conditions. However, because stabilisation of the visual image might not be as important during walking as during reading, the respective stabilisation mechanism might not have been at work. Mean head stabilisation with respect to earth, as given by the regression slope of head versus trunk angle, was found to be approximately 0.5. This value would have been 0 for correct stabilisation and 1 if the head were fixed to the trunk. Large interindividual variations, ranging from 0.1 to 0.8, also suggest that head stabilisation in the frontal plane might be not very important in linear goal-directed locomotion.

Conclusions

The fact that our fully compensated LD subjects, despite their balance problems, were able to reproduce a previously seen distance by walking leads to the conclusion that idiothetic information can be sufficient for linear distance estimation in this simple locomotor pointing task. Especially the performance of the neuroma patient, who could reach the target almost as well as a normal subject, shows that the vestibular system is not necessary for linear goal-directed locomotion. This conclusion is also supported by recent experiments (Mittelstaedt and Glasauer 1993) comparing distance estimation in normal active walking to that on a conveyor belt, where no vestibular information about translation is available.

The close relationship of step length and frequency to linear walking velocity could be an excellent means of estimating linear self-motion from motor commands (or proprioception) which could then be integrated to give distance information (as suggested, for example, by Mittelstaedt and Glasauer, 1993).

Furthermore, LD subjects could compensate quite well for the disturbances caused by unstable equilibrium during the walk. As the path curvature of their walks was high, the length of their walks was greater than the distance necessary to reach the target in a straight walk. Simply walking a path with the length equivalent to the target distance would lead to undershooting in the case of high path curvature. But, in fact, they even overshot the target. This suggests continuous updating of self-position estimation with respect to the planned path, or at least to the target position, followed by error correction of lateral deviations, as suggested by correct continuous pointing to a target during straight blindfolded walking (Loomis et al. 1992). For normal subjects, the ability to compensate for unpredictably changing resistance (imposed by a rubber band attached to the body of the subject) during walking has been shown by Corlett et al. (1990), as long as the resistance changes were relatively small. Moreover, voluntary changes in step length required by the experimenter during the walk did not change the performance, whereas involuntary disturbances imposed by the tension of a rubber band between the legs did. This would indicate the use of motor commands, rather than proprioceptive or vestibular signals, to determine self-position during the walk. Obviously our LD subjects did not succeed perfectly in error correction, as demonstrated by their larger lateral errors. As mentioned above, lack of canal information might be the reason for this inferior correction ability.

Further experimentation involving body rotations during more complex tasks, such as return walks or reproducing curved paths, will examine the role of the vestibular system in active human path integration in general. Interaction of vestibular and proprioceptive feedback for path integration might be necessary in those tasks and hence yield different results in terms of performance errors.

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