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RESEARCH ARTICLE

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Differential effects of labyrinthine dysfunction on distance and direction during blindfolded walking of a triangular path

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Abstract While we walk through the environment, we constantly receive inputs from different sensory systems. For us to accomplish a given task, for example to reach a target location, the sensory information has to be integrated to update our knowledge of self-position and self-orientation with respect to the target so that we can correctly plan and perform the remaining trajectory. As has been shown previously, vestibular information plays a minor role in the performance of linear goal-directed locomotion when walking blindfolded toward a previously seen target within a few meters. The present study extends the question of whether vestibular information is a requirement for goal-directed locomotion by studying a more complex task that also involves rotation: walking a triangular path. Furthermore, studying this task provides information about how we walk a given trajectory, how we move around corners, and whether we are able to return to the starting point. Seven young male, five labyrinthine-defective (LD) and five age- and gender-matched control subjects were asked to walk a previously seen triangular path, which was marked on the ground, first without vision (EC) and then with vision (EO). Each subject performed three clockwise (CW) and three counterclockwise (CCW) walks under the EC condition and one CW and CCW walk under the EO condition. The movement of the subjects was recorded by means of a 3D motion analysis system. Analysis of the data showed that LD subjects had, in the EC condition, a significantly larger final arrival error, which was due to increased directional errors during the turns. However, there was no difference between the groups as regards the overall path length walked. This shows that LD subjects were able to plan and execute the given trajectory without vision, but failed to turn correctly around the corners. Hence, the results demonstrate that vestibular information enhances the ability to perform a planned trajectory incorporating whole body rotations when no visual feedback is available.

Keywords Locomotion · Navigation · Path integration · Vestibular system · Triangular trajectories

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Introduction

Triangular path completion is one of the standard paradigms used to investigate path integration. Usually, the subject is guided away from the starting point, then turned, guided along the second segment of the triangle, and then asked to point or return to the starting position. In animal studies, this paradigm was successfully used to show the capability of homing, i.e., returning to the nest (gerbils: Mittelstaedt and Mittelstaedt 1980, 1982; hamsters: Etienne et al. 1988; spiders: Mittelstaedt 1985; ants: Müller and Wehner 1988). Although the ability of humans to complete a triangular path has already been shown (Worchel 1952; Klatzky et al. 1990; Mittelstaedt and Glasauer 1991; Loomis et al. 1993; Marlinsky 1999), the question of the relative contribution of sensory systems and internal mechanisms of trajectory representation remains open. If all positional information, i.e., visual and auditory cues or variations of the ground surface, is excluded, idiothetic information has to be used (idiothetic information is defined as spatial information which can only be gained by self-motion; Mittelstaedt and Mittelstaedt 1980). It is composed of different modalities: proprioceptive afference from the legs, vestibular information about translatory and rotatory accelerations, and efference copy information about the intended motion. Triangle completion requires that the current position and direction with respect to the starting point are updated from this information while walking, and that the path back to the starting point is computed from it. It does not require, however, that the path itself, or an intermediate position, is represented in the brain, since representation of two distinct variables is sufficient (Mittelstaedt 1985): these variables can be given either as the two polar components or as the two Cartesian components of a homing vector. In the first case, distance and direction are the coded variables. In the second case, two distances would be represented, for example, one along the straight ahead direction and the other perpendicular to it. The same holds if only one target has to be approached, as in the classic experiment of Thomson (1980) in which subjects had to walk toward a previously seen target (for further studies see, for example, Rieser et al. 1990; Mittelstaedt and Glasauer 1991; Glasauer et al. 1994; Mittelstaedt and Mittelstaedt 2001).

A more complex task, which necessarily requires a mental representation of the path, is to reach more than one target (Loomis et al. 1992). In this case, either map-like information (survey representation of at least the targets) or a sequence of movements to be performed (route representation) must be stored. However, it cannot be determined from such a task whether the internal representation of the path is coherent, i.e., whether the subject would find the way back to the starting point even if he/she missed the targets. This is, however, the case in the classic triangle completion task: if, for example, distance errors are made equally during the outward walk and the walk back home. A subject misestimating the distance by a certain factor on all path segments but turning correctly will nevertheless return perfectly to the starting point. A combination task including both reaching a target and homing has not been extensively examined yet, although it promises to reveal much more information about the underlying mechanisms than each task separately. Such a task would avoid the drawbacks of triangle completion but keep both the advantages of a homing experiment and of a reaching task. An example of such a task is reproduction of a previously seen triangular path. In this case, errors can be determined for both the target corners and the return walk.

Glasauer et al. (1994) showed that bilateral labyrinthine-defective (LD) subjects are able to perform linear goal-directed locomotion toward a memorized target, although the absence of canal information induced more instability during blind walking (i.e., increased path curvature). Takei et al. (1996) found that, during circular walking in darkness, a unilateral LD patient could correctly walk the required distance, but showed a direction-specific asymmetry in reproduction of the required angle. The authors suggested that unilateral lack of vestibular function may have affected walking performance. The present study, a follow-up of these previous studies, addresses two questions: (1) does vestibular information about rotation contribute significantly to the control of performing a planned trajectory by walking, and (2) are distance and direction coded separately? Another recent study conducted on unilateral vestibular defective patients (Péruch et al. 1999) used different locomotor paradigms (path reproduction, path reversal, taking a shortcut) to assess the first question, and found that patients indeed showed increased turn errors 1 week after unilateral vestibular lesion, but that this impairment vanished after about 1 month of recovery.

In the following, we give a quantitative description of the locomotor patterns and the performance of walking a previously seen triangular path with and without vision. A preliminary account of this work was given elsewhere (Viaud-Delmon et al. 1997; Berthoz et al. 1998). The same experimental protocol was also used previously in a study comparing the performance of astronauts before and after space flight (Glasauer et al. 1995).

Materials and methods

Subjects and procedure

Seven young subjects (in the following called YOUNG subjects; all male, aged 18–36 years) and five patients with vestibular deficits (in the following called LD subjects; two patients with unilateral left vestibular loss, a 46-year-old woman and a 47-year-old man; three bilateral deficient women, 27, 64 and 65 years old) participated in the first part of the study conducted in a large gymnasium in Paris. In the second part of the study, a control group of five age- and gender-matched normal subjects (in the following called CONTROL subjects) was tested in a large gymnasium in Munich. In both parts of the study the same protocol (see below) was used.

The unilateral deficient subjects (uLD) underwent operations for left-sided acoustic neurinoma, one bilateral deficient subject (bLD) had bilateral areflexia due to aminoglycoside toxicity, and the two other bLDs suffered from bilateral loss due to unknown causes. The patients underwent clinical testing of vestibular and auditory function (ENT Department, Hôpital Lariboisière, Paris) by the following methods: audiometry, caloric testing, eye-head coordination, and gaze stabilization in the frontal plane (Freyss et al. 1988). None of the bLD patients responded to the clinical vestibular tests. The symptoms of all patients had appeared at least several months before the study. All patients had undergone vestibular rehabilitation treatment (A. Semont) and were tested at the end of rehabilitation. Hence, our LD subjects can be regarded as well compensated. The local ethics committees approved the experiment, and all subjects gave their informed consent to participate.

The subjects were asked to walk unguided a previously seen triangular path first without vision (EC) and then with vision (EO). The verbal instructions given were, "Walk at a comfortable pace, as accurately as possible around the path. The motion should be continuous. The goal is accuracy, with accuracy defined as your ability to 'straddle' the path." The path was marked on the ground by a cross at each corner and consisted of a right angle with two 3-m-long segments (second corner 135°). The task was to go in alternating clockwise (CW) and counterclockwise (CCW) directions, but always to approach the right angle of the triangle first. The subjects were asked to walk the path in both directions 3 times EC and then 1 time EO. When the path was completed, the subject

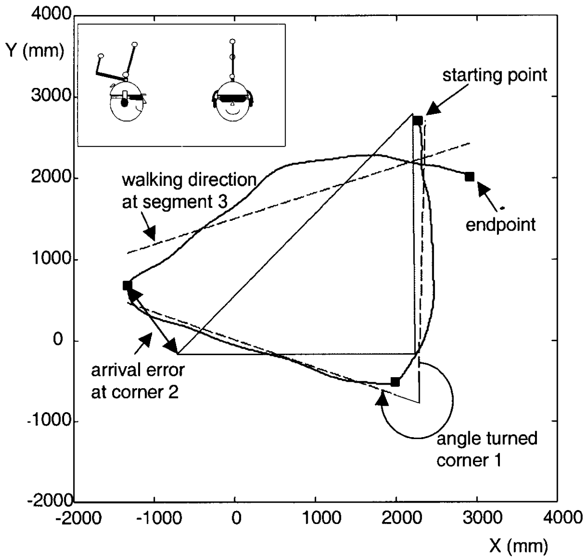

Fig. 1 Example of the trajectory of a CW walk (starting at the *upper right corner*) to illustrate different parameters of the data analysis. The *triangle* is shown as a *solid thin line*, the actual trajectory as a *solid thick line*. The *filled squares* denote corner points as determined by the trajectory. The arrival error is the distance between the corner point and the respective triangle corner. The *dashed lines* show the mean walking direction for each segment; the angle between two walking directions is used to compute the angular error (see "Materials and methods"). The *inset* shows the headset of the subject: three infra-red reflexive markers were fixed to the helmet; headphones and blackened goggles were used to mask out auditory cues and occlude vision

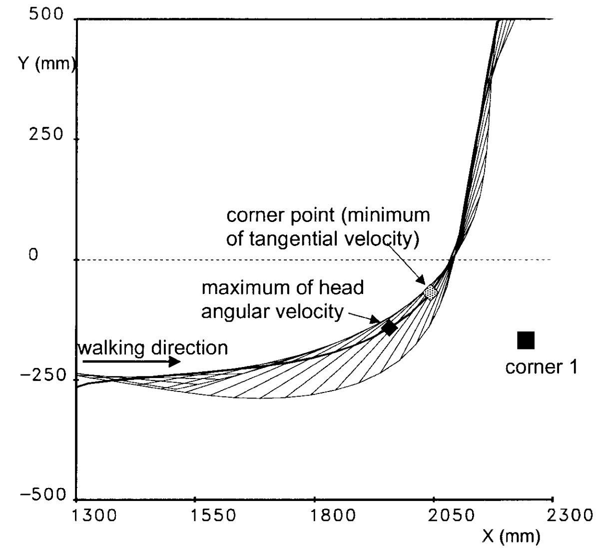

Fig. 2 Example of part of a CCW EC walk of a YOUNG subject at the first corner (*black square*) to illustrate parameters determined at each corner. The corner point, determined as minimum tangential velocity of the trajectory (*thick solid line*), is shown as a *hatched diamond*. The *black diamond* shows the maximum head angular velocity which precedes the corner. The lines connecting the two head markers (*front and back*) show that the orientation of the head changes well in advance of the corner (lead in head turning)

was requested to turn and face the starting direction again. After completion, the subjects were guided to the new starting position on a curved path to exclude any feedback information about their performance. Subjects were then instructed to look at the path before starting each EC trial. This pause (taking off the blindfold, inspecting the triangle, putting back on the blindfold) also provided sufficient time to exclude postrotational aftereffects. In the first part of the study, subjects wore a helmet with three infrared-reflective markers located above the head in approximately the sagittal plane (see Fig. 1, inset). This helmet was also equipped with headphones that provided white noise to mask out spatial auditory cues and blackened goggles to occlude vision. Two additional markers were fixed to the shoulders of the subject. In the second part of the study (CONTROL group), only one single infrared-emitting marker was attached directly to the headphones.

Before the experiment started, LD subjects were guided with eyes closed about the room at random until they felt confident with walking without vision, using the classic guiding technique for the blind: the subject firmly held the arm of the experimenter, who walked alongside to guide him/her. Although firmly guided at the beginning of this phase, the patient was progressively given more and more autonomy until he/she could walk alone. The experimenter closely followed to ensure that falling or bumping into the walls was prevented.

Data acquisition and analysis

For the YOUNG and LD subjects, the three-dimensional trajectories of the infrared-reflective markers fixed on the helmet were recorded using a video-based motion analysis system (Elite) and analyzed afterward. The coordinates necessary to describe head position in all six degrees of freedom were computed from the 3D positions of the markers. The three translational components were used to identify translational position and to compute linear velocity, the three rotational components to express head direction and to compute angular velocity of the head. For the CONTROL group, which had only one single marker attached to the head, no data about head direction or head angular velocity are available.

By means of an interactive graphics software package written by one of the authors, the corners (corresponding to a minimum of tangential velocity, Glasauer et al. 1995; see Fig. 2) of the walked trajectory and the maxima of the angular head velocity (except for the CONTROL group) were determined for each walk. The corner points were used to compute distance errors and mean walking velocity. In other studies (Grasso et al. 1998a, 1998b), the maximum curvature of the trajectory was used to determine the corner point. However, we chose not to use this criterion since it often leads to numerical problems if the tangential walking velocity is small. This is the case for the start and the end of the walk and also at the 135° corner. Also, curvature depends much more on measurement noise since it is necessary to compute accelerations, as the following considerations demonstrate. The curvature of a trajectory is given by:

$$K = \frac{\omega}{v}$$

where ω is the angular velocity and v the tangential velocity of the trajectory. Since $\omega = \frac{\dot{x}\cdot\ddot{y}-\dot{y}\cdot\ddot{x}}{v^2}$ and $v = \sqrt{\dot{x}^2+\dot{y}^2}$, both criteria will coincide as long as $\dot{x}\cdot\ddot{y}-\dot{y}\cdot\ddot{x} < v^3$ holds throughout the corner part of the trajectory. Thus, we chose the minimum of tangential velocity as the criterion for determining the subjective corner points. For an example of the tangential velocity and trajectory curvature, see Fig. 3.

To evaluate the mean walking direction for each segment of the triangle, lines of minimum least square distance were fitted to the trajectory between the corners (see Fig. 1). The angle between two consecutive lines was used to determine the amount of turn performed by the subject. The angular deviation from the desired trajectory (i.e., from the triangle's segment) was computed as the difference between the angle turned and the required angle of turn at the respective corner.

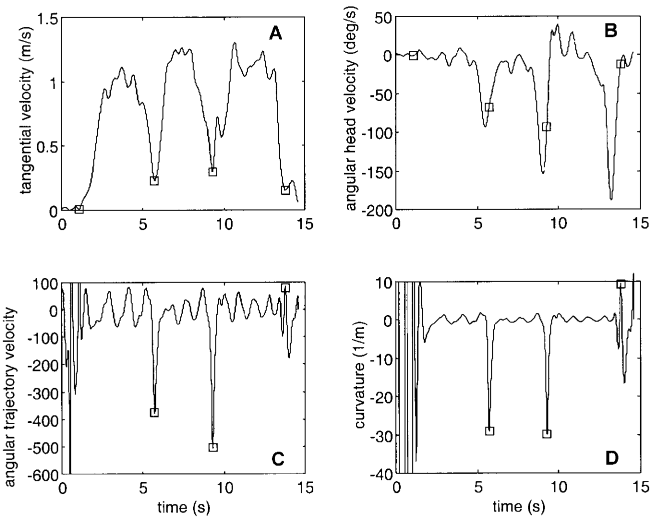

Fig. 3A–D Example of walking dynamics for a EC walk of one LD subject. The *squares in each graph* show the corner points determined as local minima of the tangential walking velocity. **A** Tangential velocity; **B** angular head velocity; note that the minima of angular head velocity are well before the corner points; **C** angular velocity of the trajectory (see "Materials and methods"). **D** Curvature of the trajectory; the minima of the curvature match the corner points for corners 2 and 3. For start and end, curvature becomes undetermined due to the low tangential velocity

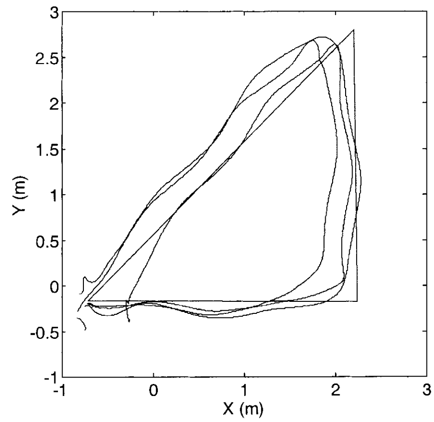

Fig. 4 All three EC CCW walks of a YOUNG subject showing larger arrival errors at corners 1 and 2 than at the endpoint. This subject overestimates the walked distance for all three segments, therefore missing the two first corners but returning almost correctly to the starting point

Two types of distance errors were computed: (1) the length error, the difference between the distance between two detected corner points and the length of the respective triangle segment, and (2) the overall length error as difference between the walked overall length and the required length (10.24 m). The arrival error, the distance between the corner point and the triangle corner (see Fig. 1), was computed as a measure of performance in reaching the corners. Thus, arrival error was cumulative over the segments and was affected by angular errors, while length errors, which described only walked distance, were not.

Due to marker dropouts, not all parts of the trajectory were successfully recorded in all trials. The incomplete parts were marked as being invalid and not used for the statistical analysis, which was performed on the mean parameter values of each subject. The ANOVA design used was a repeated measures four-way ANOVA with one between-subjects factor (subject group) and three within-subjects factors (vision, i.e., eyes open/closed, walking direction, and triangle segment), if not stated otherwise. uLDs and bLDs were treated as one group since our primary question was whether accurate vestibular feedback is necessary to reproduce a previously seen path without vision.

Statistical analysis was performed using the Statistica software package (Statsoft Inc., Tulsa, USA, 2001).

Results

As described in "Materials and methods," four points were determined for each walk: starting point, corner 1, corner 2, and the endpoint of the walk (see Fig. 1). The path trajectory was accordingly subdivided into three segments between these points. First, errors of path length, arrival at the corners, and walking direction are described as a measure of performance. Then, several parameters characterizing the locomotion while walking around the two corners of the triangle are analyzed. Subjects showed large interindividual differences for all of the parameters, but visual inspection showed that intraindividual differences were small (see Fig. 4 for an example), demonstrating a good repeatability. As an example of the overall performance, all first CW runs of YOUNG and LD subjects are shown in Fig. 5.

The age- and gender-matched group of CONTROL subjects was used primarily in determining the differences to LD subjects. However, part of the analysis was not possible for CONTROL subjects due to differences of the measurement device (see "Materials and methods"). Therefore, YOUNG subjects were included in the analysis as a separate group.

One of the YOUNG subjects showed an unusually large asymmetry between CW and CCW trials, but a clinical test of vestibular function (see "Materials and methods") revealed no disorders except for a small positional nystagmus to the right. The reason for the asymmetry was a change in turning strategy between CW and CCW trials: for CW trials, the subject did not walk around the corners but pivoted on one leg, especially for the last corner (see Fig. 5, lower left part). The relevant parts of the analysis were done with and without this subject, but since none of the statistical significances changed, all values in the "Results" include the subject.

Distance errors

The length error gives the difference between required length of a segment and actual distance covered. Thus, it is not cumulative and shows purely longitudinal errors in reproducing the segments. Additionally, the overall length error was computed for the EC condition as the difference between the required overall length (10.24 m) and the walked overall path.

Walking direction and subject group (CONTROL, YOUNG, LD) had no effect on signed length error. All

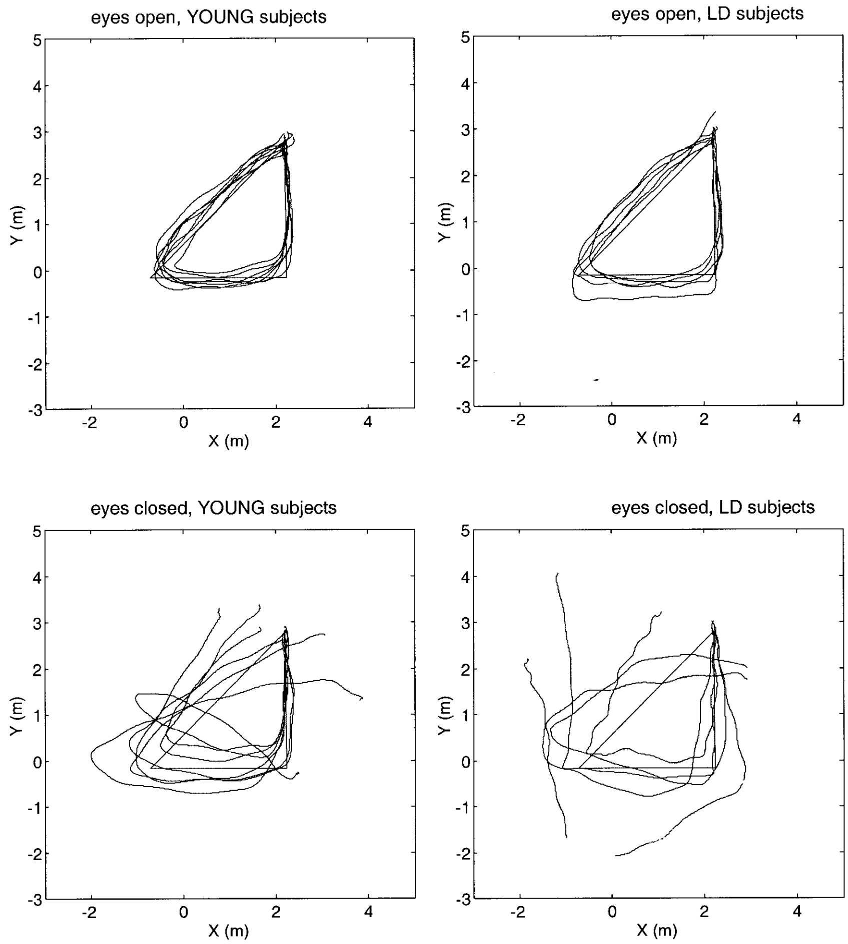

Fig. 5 Map view of trajectory of raw data for the first CW EO (*upper row*) and EC (*lower row*) runs of YOUNG (*left column*) and LD subjects (*right column*). The *triangle* shows the required path; starting point was always the upper right corner. Several qualitative observations can be made: in the EO condition (*upper row*): (1) YOUNG subjects walk more smoothly than LD subjects, but (2) tend to cut the corners more than LDs. In the EC condition, (3) LD subjects make larger directional errors, especially on the last segment of the triangle. However, one YOUNG subject showed a large error on the last segment (see "Results"). (4) The overall path length does not differ between groups or subjects and is similar to the required length for both groups. (5) YOUNG subjects make smoother corners and walk more stably as indicated by their straight trajectories

subjects, whatever their group, show almost correct average segment length (M=0±63 cm) when walking EC, and undershot slightly EO (M=–26±31 cm). This result [$F_{(1,14)}$=6.27, P=0.025] is due to the fact that subjects performed smoother trajectories when walking with vision (see Fig. 5, upper row), i.e., they rounded corners rather than walking sharp triangular turns (see also below, path curvature). Segment had a significant effect [$F_{(2,28)}$=3.79, P=0.035], which was not caused by different segment lengths but because all subject groups undershot the second segment independent of vision as indicated by the missing interaction of vision and segment.

The unsigned (absolute) length error was also evaluated to examine whether effects may have canceled out due to differences in over- or undershooting within subjects or groups. However, as for signed errors, subject group had no effect. A significant effect of visual condition [$F_{(1,14)}$=4.84, P=0.045] revealed that absolute length errors slightly increased while walking eyes closed. Also, absolute length errors increased significantly with segment number [$F_{(2,28)}$=8.48, P=0.001], showing higher errors with eyes closed, as revealed by interactions of segment and visual condition (see Fig. 6A). The main effects were, however, caused by segment 3 being longer than 1 and 2, since relative absolute length errors showed no main effects. The remaining significant interaction between vision and segment [$F_{(2,28)}$=5.01, P=0.014] was due to a smaller relative absolute length error at segments 1 and 3 with EO than with EC.

Subject group had no effect on overall length error. This was expected from the length error results above. Overall, subjects undershot with EO and overshot EC [$F_{(1,14)}$=6.85, P=0.020] (EC: YOUNG 79±195 cm, CONTROL –35±126 cm, LD 146±105 cm). Finally, a significant interaction of walking direction and subject group [$F_{(2,14)}$=3.78, P=0.049] accompanied by an effect of vision × direction × group [$F_{(2,14)}$=4.25, P=0.036] was due to CONTROL subjects in EC walking shorter for CCW than CW, while both LD and YOUNG showed the opposite.

Arrival error

The arrival error (see Fig. 1) describes the distance of each corner point to the required corner at the end of a segment. Thus, arrival error is an absolute estimate, including the effects of both directional and longitudinal deviations from the required path. Note that arrival error is cumulative over the walk, while length error is not.

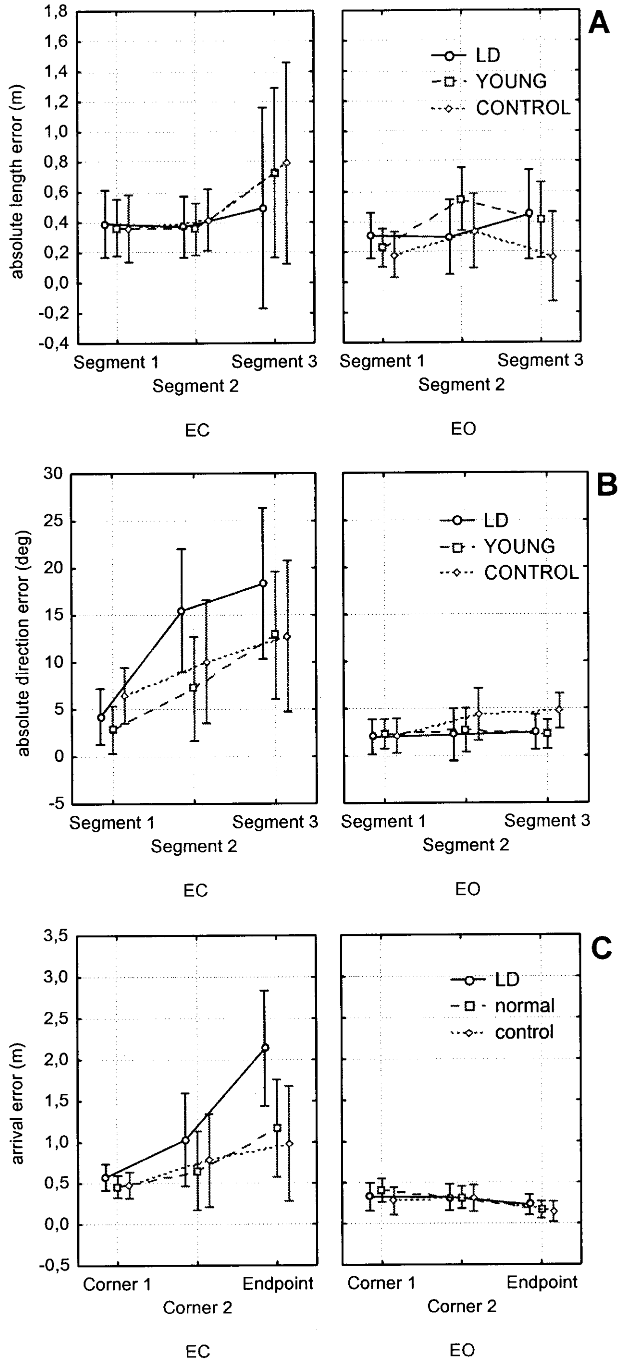

Fig. 6 Absolute length errors (**A**), absolute directional errors (**B**) and arrival errors (**C**) plotted over segment (*x*-axis) for EC (*left column*) and EO (*right column*) for all subject groups (*line patterns*). *Bars* denote 95% confidence intervals. **A** Absolute length errors increase with segment length for the EC condition, but show no effect of subject group. **B** Absolute directional errors increase for the EC condition, with LD subjects showing the largest errors. **C** Arrival error increases for all three subject groups with segment under EC conditions. While CONTROL and YOUNG subjects show similar performance, the larger arrival errors for LD subjects at corner 2 and endpoint are caused by the increased directional errors

Table 1 Arrival error (m) ± SD at the two corners and the endpoint for walking without vision (EC) for all three groups of subjects

	YOUNG	CONTROL	LDs
Corner 1	0.46±0.18	0.48±0.27	0.57±0.21
Corner 2	0.65±0.46	0.77±0.44	1.03±0.61
Endpoint	1.17±0.83	0.98±0.50	2.14±1.03

The arrival error was computed for the two corners and the endpoint of the walk (see Table 1 and Fig. 6C). The arrival error at the endpoint of the walk is the best indicator of the overall performance of the subjects and will therefore be analyzed separately. Subject group had a significant effect [$F_{(2,14)}$=7.51, P=0.006] under the EC condition; LD subjects showed a much larger error than CONTROL or YOUNG (see Table 1 for values). No such effect was found for the EO condition [$F_{(2,14)}$=1.12, P=0.35, NS]. Direction had no significant effect. As evident from the length errors, the difference in endpoint arrival error cannot be attributed to misestimating walked distance; rather it must stem from errors made during the turns, as shown below ("Directional errors").

Analyzing arrival error for all three segments and both vision conditions revealed significant main effects of subject group [$F_{(2,14)}$=4.44, P=0.032], vision [$F_{(1,14)}$=74.4, P<0.001], and segment [$F_{(2,28)}$=23.4, P<0.001]. Walking direction had no effect. With EC, LDs showed the largest overall errors (M=125±95 cm) compared to CONTROL (M=74±46 cm) and YOUNG (M=76±62 cm). The highly significant interaction between vision and segment [$F_{(2,28)}$=56.5, P<0.001] was due to increasing errors with segment in EC for all subjects. The significant interactions between subject group and vision [$F_{(2,14)}$=4.44, P=0.032], subject group and segment [$F_{(4,28)}$=5.23, P=0.003], and subject group × segment × vision [$F_{(4,28)}$=4.36, P=0.007] confirmed the observations shown in Table 1 and Fig. 6C: with EC, LD subjects showed much higher arrival errors than CONTROL and YOUNG for corner 2 and the endpoint.

Two of the seven YOUNG subjects showed, with EC, smaller arrival errors at the endpoint than at the preceding corners for one walking direction. For one of them, this was clearly due to an overestimation of walked length on all three path segments (see Fig. 4): this subject was able to come back to the starting point despite missing the previously seen visual targets, which can be attributed to misestimation of walked distance.

Directional errors

The directional error is given as difference between the mean walking direction during each segment with respect to the previous segment and the required angle of turn from one segment to the next (see Fig. 1). Hence, it is not cumulative over corners.

Signed directional errors showed no significant main effect. However, it is interesting to note that the two uLD

Table 2 Absolute directional error [deg] ± SD at the three segments for walking without vision (EC) for all three groups of subjects. Directional error at segment 1 is the deviation from the straight ahead direction

Segment	YOUNG	CONTROL	LDs
1	2.8±2.3	6.5±5.0	4.2±3.6
2	7.2±5.1	10.1±7.9	15.3±13.5
3	12.8±12.0	12.8±8.8	18.4±9.7

subjects showed an opposite effect of walking direction on signed directional error, even though their lesion was on the same side. This might possibly be due to an asymmetric walking behavior occurring before the vestibular deficit (Boyadjian et al. 1999). Indeed, we observed such an asymmetry for one "atypical" YOUNG subject (see Fig. 5, lower row).

Therefore, we examined the absolute directional errors for each path segment (see Table 2 and Fig. 6B). As expected, this error was negligible for EO (M=2.8±2.3°), but it increased significantly [$F_{(1,14)}$=104.75, P<0.001] for the EC condition (M=9.7±9.5°). Also, a significant effect of segment was observed [$F_{(2,28)}$=25.44, P<0.001], which is due to increasing errors during the EC condition as revealed by the interaction of visual condition and segment [$F_{(2,28)}$=17.02, P<0.001]. This increase in absolute directional errors during EC was linked to the amount of directional change to be performed during the walk (M=4.3±3.9° for the straight-ahead path segment; M=10.4±9.5° for the 90° corner, M=14.4±10.7° for the 135° corner). Over all conditions, subject group had no effect [$F_{(2,14)}$=3.36, P=0.064). However, as shown by a significant interaction of visual condition and subject type [$F_{(2,14)}$=5.30, P=0.019], this is due to the good performance of all subjects with eyes open. For EC only, effect of subject group on the absolute directional error was significant [$F_{(2,14)}$=4.32, P=0.034] with LD subjects showing the largest errors at segments 2 and 3 (see Table 2). This led to their larger arrival errors described above.

Path parameters: velocity and curvature of walking

Mean walking velocity was computed by dividing the walked length by time needed for one segment to be walked. All subjects walked significantly [$F_{(1,14)}$=35.0, P<0.001] slower without vision (M=0.79±0.17 m/s) than with vision (M=0.88±0.14 m/s). While there was no overall effect of subject group, it became significant [$F_{(2,14)}$=4.12, P=0.039] for the EC condition where YOUNG subjects walked slightly faster (M=0.88±0.15) than LD (M=0.75±0.16) and CONTROL (M=0.67±0.15). All subject groups walked fastest for segment 2, with a significant effect of segment [$F_{(2,18)}$=19.35, P<0.001].

To assess path curvature, the mean deviation from the straight line between the corner points was computed for each segment of the triangle. Overall, there was a significant effect of subject group [$F_{(2,14)}$=5.83, P=0.014] and segment [$F_{(2,28)}$=24.0, P<0.001]. As revealed by the interaction of segment and subject group [$F_{(4,28)}$=5.02, P=0.004], this, unexpectedly, was due to the CONTROL subjects who showed a higher curvature for the second segment. This finding is explained by the smoother walking of CONTROL subjects as compared to the other groups.

Corner parameters

The following parameters were computed for the 90° (first turn) and 135° (second turn) triangle corners only. Tangential linear velocity at each corner was, independent of visual condition, slightly different between subject groups [$F_{(2,14)}$=3.75, P=0.0498], with YOUNG subjects taking the corners faster than the other groups. As expected, all subjects slowed down more for the second (larger) turn [$F_{(1,14)}$=124.5, P<0.0001].

Since head angular velocity could not be measured in the CONTROL group, the following analysis is based on YOUNG and LD subjects only. For both groups, the tangential linear velocity turned out to be a minimum at the corner point (see data analysis) preceded by a maximum of angular head velocity (see Fig. 3 for a representative example). This means that prior to walking around the corner the subjects turned their head in the new direction (see Fig. 2).

Regardless of the vision condition, all our subjects showed a significantly [$F_{(1,10)}$=59.11, P<0.0001] larger maximal angular head velocity when negotiating the 135° turn (M=134±34°/s) than they did with the 90° turn (M=99±25°/s). In parallel, this was accompanied by a tangential velocity with a significantly [$F_{(1,10)}$=94.19, P<0.0001] smaller amplitude for the 135° turn (M=0.47±0.17 m/s) than for the 90° turn (M=0.78±0.24 m/s). Our subjects showed a significant [$F_{(1,10)}$=18.58, P=0.002] decrease in their maximum head angular velocity at a turn, when walking EC (M=111±35°/s) than when walking EO (M=127±32°/s). Without vision, LD patients showed significantly [$F_{(1,10)}$=7.75, P=0.02] lower head turn velocities (M=92±28°/s) than did YOUNG (M=123±33°/s).

We observed neither an effect of the presence of vision nor an effect of subject group (YOUNG vs LD) on mean tangential velocity or head anticipation (head lead time) at a corner (see Fig. 2 for an example). However, a test of the homogeneity of variances of head lead time of the two groups of subjects (YOUNG and LDs) revealed a significant difference of the standard deviations (P=0.002), with LDs being more variable.

Discussion

Linear and angular components of a triangular walk

Thomson's (1980) experiment on "locomotor pointing" was the first to examine the reproduction of a previously seen trajectory without vision. Most of the work since then has concentrated on walking toward one target. For two different segments, one straight ahead and the second perpendicular to it, Loomis et al. (1992) showed that subjects are able to reproduce previously seen distances correctly by walking. Our results support this: the observed overall path length is not significantly different from the required overall distance to be covered.

As regards our question on whether the vestibular system as inertial sensor contributes to path integration, previous experiments (Glasauer et al. 1994) already showed that the vestibular organ does not significantly contribute to the estimation of active linear self-displacement. Our current results again support this: linear self-displacement, i.e., the overall distance walked, was close to the required distance and not significantly different between healthy subjects and patients. Also, the arrival error at the first corner was not significantly different between subject groups. Thus, the significantly larger arrival error at the endpoint of LD patients has to be attributed to the remaining component of triangular walking: angular errors. This is indeed confirmed by the larger directional error of LD patients. Since LD subjects and our age- and gender-matched CONTROL subjects walked equally fast, the differences between the groups cannot be attributed to different walking velocities, which are known to influence path integration capabilities (Rieser et al. 1990; Mittelstaedt and Glasauer 1991; Mittelstaedt and Mittelstaedt 2001). This result contradicts Worchel's finding (Worchel 1952) on triangle completion: in his study, labyrinthine-deficient subjects performed better than normal subjects. He attributed this to a disturbing influence of the semicircular canal stimulation during triangular walks. Similarly, Péruch et al. (1999) found that compensated unilateral vestibular defective subjects performed equally well to normal subjects in various locomotor tasks such as path reproduction or taking shortcuts.

Our results, in contrast, suggest that the information about the angle turned at a corner cannot be sufficiently measured by proprioception or inferred from the motor commands, but it has to be enhanced by angular velocity information from the semicircular canals. Since neither age nor gender can explain the differences found between LD patients and CONTROL or YOUNG subjects, these differences can only be attributed to the presence or absence of correct vestibular information about self-rotation. This is in line with the suggestion of Takei et al. (1996) derived from the results of one unilateral LD patient during circular walking. The contradicting result of Péruch et al. (1999), who found increased turn errors in unilateral LD patients only 1 week after vestibular nerve lesion, but not later, may be due to a difference in experimental protocol. While subjects in the study of Péruch et al. (1999) were required to either turn or walk straight, i.e., to turn in place, subjects in our study were explicitly asked to perform a natural movement, i.e., to walk smoothly around the corners of the triangle.

In our study, both unilateral and bilateral LDs showed increased absolute angular errors and arrival errors compared to healthy subjects. The directional asymmetry of the unilateral LD subjects who had the lesion on the same side was, however, opposite. Thus, further studies with more patients would be required to specify the effects of unilateral vestibular failure on angular performance in goal-directed locomotion.

One of our normal subjects also showed a specific asymmetry for CW and CCW walks (see Fig. 5), which was due to a change in strategy: the subject pivoted on one leg for CW walks instead of really walking around the corner. Differences in leg length or strength may be another reason for directional asymmetries found in normal subjects (Boyadjian et al. 1999). The results of our subject for distance-related variables were not different from those of other subjects. Apparently, walking strategy plays an important role in blind locomotion, but ineffective strategies for body rotation do not necessarily affect distance evaluation.

While a task such as triangle completion necessitates that proprioceptive and/or vestibular sensory information is collected during the outward path to infer the homing path, in our paradigm subjects could theoretically rely exclusively on a pre-planned locomotor program. Such a locomotor program could indeed be one reason for the exceptionally good performance of our subjects for the linear components of triangular walking. For linear blindfolded walking, Fitzpatrick et al. (1999) showed that sensory feedback can be used: some subjects corrected for disturbances applied by galvanic vestibular stimulation, while others continued to walk in the wrong direction. According to our results, pre-programmed locomotion appears not to be the preferred strategy for the directional components of the walk, since the missing vestibular feedback of our LD patients influenced walking performance.

Walking the triangle: the corners

While walking around corners, head motion is coordinated with the position along the trajectory: the head precedes the turn by 200–300 ms (Glasauer et al. 1995; Grasso et al. 1996, 1998a, 1998b; Imai et al. 2001). The anticipatory head turning is also observed in darkness, which suggests that it not only serves visual control of the trajectory. Head anticipation has also been observed during locomotion along circular paths (Grasso et al. 1996) and also during postural recovery where the head is followed by the trunk. This suggests that the brain exercises predictive control on the locomotor trajectory.

In the present study, similar times for normal and LD subjects were found, but the variability of the head lead time of LD subjects was significantly larger, suggesting a disrupted coordination between head movement and trajectory formation. In normal subjects, the head rotates before the corner is walked. LD subjects showed the same pattern, but with a much larger variety in timing.

Hypothetically, the coordination of head turn and walking could be disrupted in LD subjects, because the vestibular organ can no longer act as sensor to perceive the turn. Thus, the coordination is no longer required. This hypothesis is supported by the very high standard deviation of LD subjects under the EC condition compared to that under the EO condition, where it is useful to direct gaze along the planned trajectory (Grasso et al. 1998b), and where visual information is available for gaze readjustment.

All subjects showed larger head turn velocities and smaller walking speed when negotiating the second corner than they did for the smaller angle at the first corner. Thus, walking speed and turning of the head are apparently both adapted to the angle of turn to be performed.

We suggest that the accurate execution of the planned turn but not the walked distance is monitored by sensory input from the vestibular system which is used to correct for errors if no visual information is available. Such a corrective feedback may help healthy subjects even in everyday locomotion if visual feedback is degraded (darkness, fog, etc.) or is temporarily unavailable due to occlusion of the goal or distracted visual attention.

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