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Supplemental Data

Walking Straight into Circles

Jan L. Souman, Ilja Frissen, Manish N. Sreenivasa, and Marc O. Ernst

Supplemental Experimental Procedures

Forest Trajectories

Walking data were collected in the Bienwald, a large flat forested area on the border of Germany and France. Undergrowth density varied and several narrow creeks cut through the forest. Two start locations were used: N49°00.914'; E8°09.380' and N49°01.440; E8°09.430' (see Fig. 1A). Data were collected on three different days (15-16 August 2007, with cloudy weather, and 1 October 2007, with sunny weather). Six students from the Eberhard Karls University of Tübingen (1 female; age 21-32) were paid for their participation. None of them had been to this area before. They were instructed to follow the direction indicated to them at the beginning of their walk as accurately as possible, without the aid of any navigational instruments (including their watch). Walking trajectories were recorded at 1Hz by a GPS receiver worn by the participant (Garmin GPSMAP 76 CSx). An experimenter followed the participant at close distance, both for safety and to ensure that no navigational instruments would be used. Participants walked 3½ (PS and MJ) or 4 hours and covered between 8.9 and 12.5 km.

Desert Trajectories

The desert experiment was conducted in collaboration with Buckle-Up Productions (Essen, Germany), who filmed two of the walks (KB and SK) for the popular German science television program Kopfball (Westdeutscher Rundfunk; the film, in German, can be downloaded at http://medien.wdr.de/download/1174318097/kopfball/wdr_fernsehen_kopfball_20071202.mp4). Care was taken that the filming did not interfere with the walking task. Walking data were collected in the Sahara desert, approximately 40 km South-West of Douz (Tunisia). Experiments were carried out from a base camp, located at N33°13.070'; E8°40.937', on 1-2 June 2007. Maximum temperature in the shade was about 45°C on the first day and 35°C on the second. During the night, the full moon was initially visible, but disappeared behind the clouds during the experiment. The terrain consisted of prototypical sand-dune desert, with occasional sparse vegetation. Care was taken to choose a location where no landmarks (mountains, trees, man-made structures) were visible to the naked eye. Participants were employees of the production company and the WDR television station (all male; ages 24, 35 and 41). They were instructed to follow the direction indicated to them at the beginning of their walk as accurately as possible, without using any navigational instruments (including their watch). Walking trajectories were recorded at 1Hz by a GPS receiver worn by the participant (Garmin GPSMAP 76CSx for KB and SK; for IK, a Garmin GPSMAP 60C was used with an automatic recording interval of about 10s, depending on recorded displacement). An experimenter followed the participant at a moderate distance (ca. 50 m for KB and IK, ca. 10 m for SK), both for safety and to ensure that no navigational instruments would be used. In addition, a camera man and a support all-terrain vehicle with driver followed KB, occasionally overtaking the participant and filming him. SK walked during the night, with a camera man following him in addition to the experimenter. IK walked with only an experimenter following him. KB walked 7.6 km in 3½ hours during the heat of the day, IK walked 11.2 km in 3 hours in the morning, and SK walked 6.6 km in 2½ hours during the night. Only these three trajectories could be recorded, because the team was forced to leave the desert by a sandstorm.

Blindfolded Walking

The blindfolded walking experiments were carried out on the airstrip of Poltringen (Germany; N48°32.7'; E8°56.75'), a large open grass field (approx. 800 x 200 m), crossed by a concrete runway. 13 Students of the Eberhard Karls University of Tübingen were paid for their participation. In addition, two of the participants in the desert experiment took part (KB and SK). Participants were instructed to walk as straight as possible in the direction indicated at the beginning of each trial by the experimenter. They were blindfolded with tightly fitting goggles, which did not transmit any light, and wore earplugs to attenuate auditory cues. On sunny days, participants wore a large hat that prevented them from feeling the sun on their face or neck. Walking trajectories were recorded at 1 Hz by GPS (Garmin GPSMAP 67CSx), carried by the participant.

The first 9 participants walked 10 trials of 5 min. To minimize feedback, they were reoriented at the end of each trial by the experimenter while still blindfolded. They then walked a short distance to a new location, where they were allowed to take off the blindfold. After this, they walked to yet another location, where the next trial started. The last 6 participants (MV, PS, SK, JS, JH, and KB) walked 5 trials of 10 min. After each trial, they were first turned around multiple times in different directions, after which they were allowed to take off the blindfold and walk to the next starting point. These six participants were tested with a longer trial duration than the first nine, to investigate whether the prolonged absence of vision would cause them to walk more in circles. Since this turned out not to be the case, the data from all 15 participants were aggregated in further analysis. During the experiment, an experimenter followed the participant at close distance and stopped him/her when the end of the grass field was reached. The participant was then reoriented while still blindfolded and continued walking.

GPS data were low-pass filtered in post-processing, using a 2^{nd} order zero phase shift Butterworth filter (cut-off frequency 0.1 Hz). When the participant was turned around at the edge of the field during a trial, the second part of the trajectory was rotated so that the direction between the last two samples before the turn and that between the first two samples after the turn was aligned. Similarly, trajectories from subsequent trials were aligned and pasted together. Veering from a straight path was expressed in the change in walking direction per second.

To analyze the effects of accumulating noise in the sensory cues for walking direction without vision [S1], all trials with at least 240 s of walking data were used (8 of the 120 trials were shorter). The starting direction of all trials was aligned and the average position in the first 240 s computed per participant. Figure 3 shows the average displacement across all participants in the initial direction (X) over time (A) and the variability of position in both the initial direction and the orthogonal direction (B).

The effect of discontinuities in the blindfolded walking task, such as trial starts and points where participants were turned around at the edge of the field (turns), was tested by computing the median values of the change in walking direction in the last 15 s before the discontinuity and in the first 15 s after it. We averaged across 15 s, because direction change values just before and after discontinuities were fairly noisy, due to the low walking speed. For each participant, these median values were transformed into standardized z-scores and then aggregated across all participants. To test for recalibration of the subjective straight-ahead, we computed the correlation between the change in walking direction before the trial start or turn with: a. the change in direction just after the trial start or turn; b. the difference between the change in direction after and before the trial start or turn. The first correlation indicates to what extent participants kept veering in the same direction, while the second correlation expresses the amount of recalibration. The significance of correlations relative to zero was tested with a standard t-test, while a z-test with Fisher r-transformation was used to test the difference between two correlations for trial starts and turns.

Leg Strength Measurements

Dynamic leg strength was measured in the Sports Medicine Department of the Eberhard Karls University of Tübingen for 11 of the 15 participants in the blindfolded walking experiment (the other participants were not available for testing anymore). Maximum extension and flexion torque of the knee were measured for both legs at a constant velocity of 60°/s, using an isokinetic test device (IsoMed 2000, D&R Ferstl, Hemau, Germany).

Leg Length Manipulation

Eight of the 15 participants in the blindfolded walking experiment took part. Leg length was manipulated by adding lifts under the shoe soles. The lifts themselves were made of 235 x 70 x 6 mm pieces of cork which were stacked and glued together to obtain the required height. Lifts of 6 mm and 18 mm height were used. To attach the lifts to the shoes we customized a pair of Polar Cleats (Moonlite Crafters, Smithers, Canada) with strips of Velcro. The lift under the left foot could be either higher than that under the right foot (12 mm difference), lower (-12 mm), or equal in height (both 6 mm). Participants walked blindfolded on the runway of Poltringen airstrip (15 m wide), after seeing the target direction, and were instructed to walk as straight as possible. They did not see the lifts under their feet. All three conditions were repeated 10 times, in random order. Participants walked until they veered off the runway, or until they reached a distance of about 25 m. Walking trajectories were recorded by GPS at 5 Hz, using a NovAtel Propak V3 – L1 receiver in combination with a NovAtel - GPS 532 antenna (NovAtel, Calgary, Canada). GPS data were logged on a lightweight tablet pc (Fujitsu LT P600). The participant carried the GPS receiver, antenna and tablet pc in a backpack. GPS data were post-processed using GPS Baseline Post-Processing software (GrafNav, NovAtel, Calgary, Canada) and converted to planar coordinates. For each participant, the average change in walking direction per distance travelled was computed for each condition. Differences between the three conditions were tested with a Repeated Measures ANOVA (SPSS 15.0).

Simulation of Blindfolded Walking

Blindfolded walking trajectories were simulated with a correlated random walk model of the subjective straight-ahead. This simulation serves as an illustration of the possible effect of accumulated noise on the blindfolded walking direction, rather than as a formal model of the data. For each step t with fixed step length l = 0.7m, a random error $\delta(t)$ was added to the subjective straight-ahead direction $\theta(t-1)$ at the previous step (see Figure S2A). The new position $[x(t), y(t)]$ was thus displaced from the previous position $[x(t-1), y(t-1)]$ by distance l and rotated over angle $\theta(t) = \theta(t-1) + \delta(t)$:

$$\begin{bmatrix} x(t) \\ y(t) \end{bmatrix} = \begin{bmatrix} x(t-1) \\ y(t-1) \end{bmatrix} + l \cdot \begin{bmatrix} \cos[\alpha(t-1) + \theta(t)] \\ -\sin[\alpha(t-1) + \theta(t)] \end{bmatrix} \quad (1)$$

where $\alpha(t\text{-}1) = \sum_{i=1}^{t-1} \theta(i)$ and positive angles refer to clockwise rotations. Deviation δ was randomly drawn from a highly peaked Von Mises distribution (the circular equivalent of a Gaussian distribution) with zero mean and concentration $\kappa = 500000$. A walk of 5000 steps with a step frequency of 1.67Hz was simulated (equivalent to 50 min. of walking, as in the blindfolded walking experiment).

Supplemental Reference

S1. Cheung, A., Zhang, S., Stricker, C., and Srinivasan, M. (2007). Animal navigation: the difficulty of moving in a straight line. Biological Cybernetics *97*, 47-61.

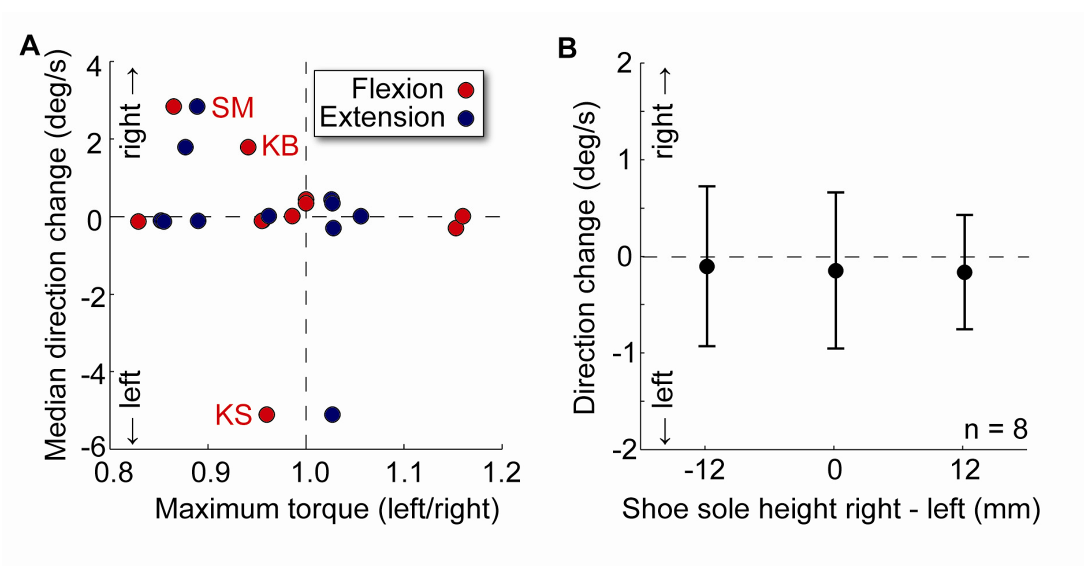

Figure S1. Biomechanical Asymmetries and Walking Direction

(A) Median direction change during blindfolded walking plotted against the ratio between left and right legs for maximum torque in flexion (red) and extension (blue), for 11 of the 15 participants in Fig. 2. Participants who consistently turned in one direction during walking are indicated by their initials.

(B) Mean change in direction as a function of difference in sole thickness in the leg length manipulation experiment. Error bars indicate the 95% confidence interval of the mean across 8 participants. The three conditions did not differ from each other significantly ($F(2,14) = 0.078$, $p = 0.925$).

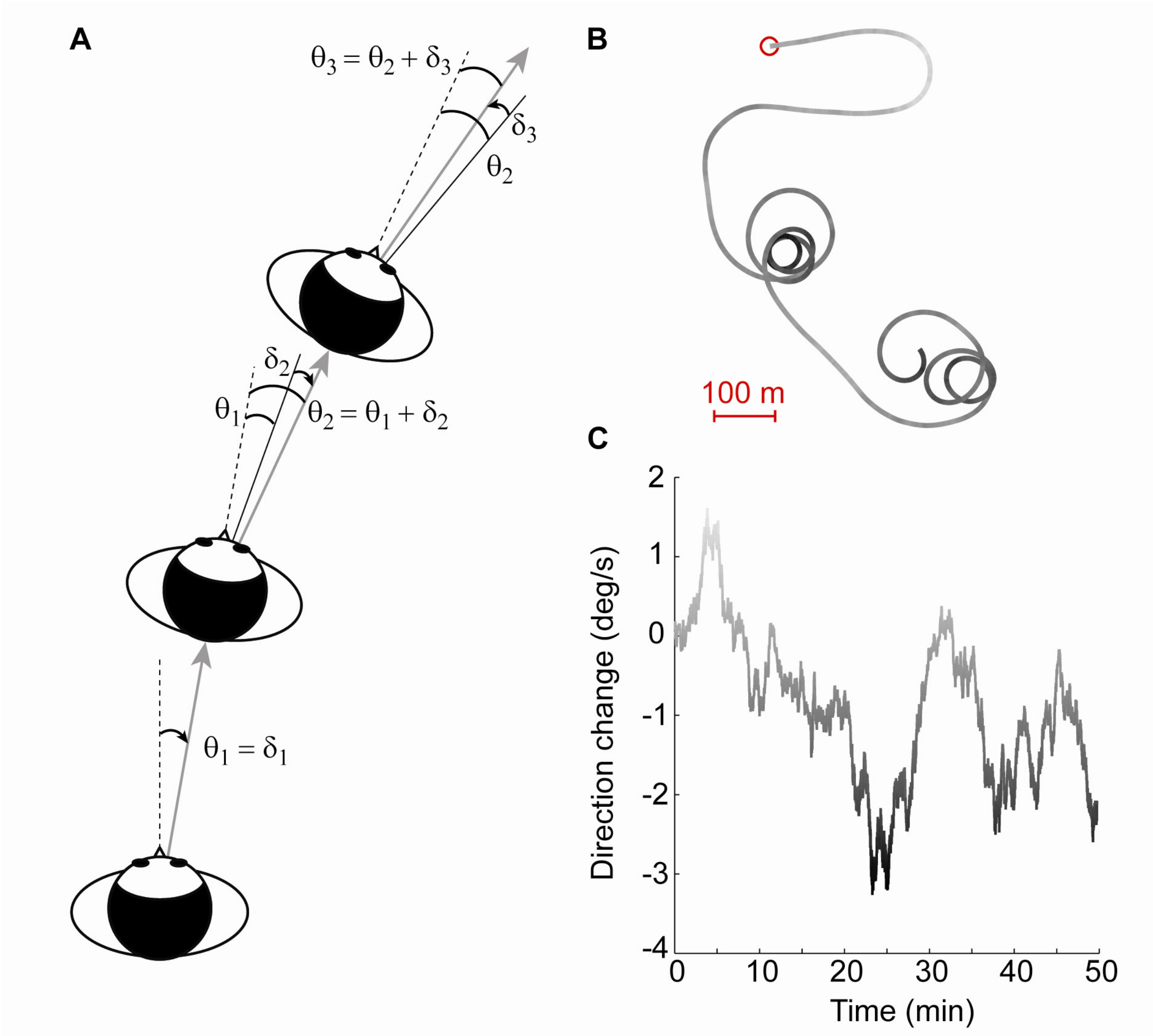

Figure S2. Simulation of Blindfolded Walking

(A) Correlated random walk model. For each step, a random deviation δ from straight-ahead is drawn from a circular normal distribution with zero mean and concentration κ, and added to the cumulative sum of the previous deviations $\theta_t = \sum_{i=1}^{t-1} \delta_i$. This subjective straight-ahead determines the direction of the next step relative to that of the previous one (grey arrows). Three steps are shown, with the initial $\theta_0 = 0$. Step length l is fixed.

(B) Example trajectory produced by the random walk model with 5000 steps. The red circle indicates the start position; grey levels correspond to the amount of change in the walking direction.

(C) Change in walking direction over time, computed from the trajectory in (B).