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RESEARCH ARTICLE

Keeping track of the distance from home by leaky integration along veering paths

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Abstract When humans use vision to gauge the travel distance of an extended forward movement, they often underestimate the movement's extent. This underestimation can be explained by leaky path integration, an integration of the movement to obtain distance. Distance underestimation occurs because this integration is imperfect and contains a leak that increases with distance traveled. We asked human observers to estimate the distance from a starting location for visually simulated movements in a virtual environment. The movements occurred along curved paths that veered left and right around a central forward direction. In this case, the distance that has to be integrated (i.e., the beeline distance between origin and endpoint) and the distance that is traversed (the path length along the curve) are distinct. We then tested whether the leak accumulated with distance from the origin or with traversed distance along the curved path. Leaky integration along the path makes the seemingly counterintuitive prediction that the estimated origin-to-endpoint distance should decrease with increasing veering, because the length of the path over which the integration occurs increases, leading to a larger leak effect. The results matched the prediction: movements of identical origin-to-endpoint distance were judged as shorter when the path became longer. We conclude that leaky path integration from visual motion is performed along the traversed path even when a straight beeline distance is calculated.

Keywords Vision · Perception · Navigation · Path integration · Optic flow · Sensorimotor · Human

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Introduction

Path integration is a mechanism by which a locomoting organism can track its location relative to a starting point or goal in the environment (Mittelstaedt and Mittelstaedt 1973). It works by integrating the movement of the organism to obtain its position. Several species of animals are known to use path integration to monitor the distance and direction from their nest during foraging and to successfully find their way back afterward (Mittelstaedt and Mittelstaedt 1980; Etienne 1992; Seguinot et al. 1993; Collett et al. 1998; Menzel et al. 2000). Humans can also use path integration to update their position during locomotion, even when they are blindfolded and have access to only proprioceptive and vestibular signals (Loomis et al. 1993, 1999; Fujita et al. 1993; Etienne et al. 1996). Vision supports path integration by providing visual motion cues about direction, speed, and duration of movement. Integrating the motion specified by these cues gives a measure of the distance traveled. Studies of visual path integration have used simulated movements in virtual environments to avoid proprioceptive and vestibular cues and to investigate vision in isolation (Peruch et al. 1997; Klatzky et al. 1998; Bremmer and Lappe 1999; Riecke et al. 2002; Kearns et al. 2002; Frenz et al. 2003).

Over distances of several tens of meters, human path integration from visual cues shows some characteristic errors. Final distances from the starting point of a movement are underestimated, such that participants report a distance that is lower than the true length of the movement (Frenz and Lappe 2005; Frenz et al. 2007; Lappe et al. 2007). At the same time, distances traveled enroute to a memorized goal location are overestimated such that participants report having arrived at the goal location even before the movement is over (Redlick et al. 2001; Lappe et al. 2007). Both findings can be explained by assuming that path integration is leaky (Lappe et al. 2007).

Leaky path integration (Lappe et al. 2007) proposes that the participant continuously tracks a state variable, such as the current distance from the starting point. The state variable is updated with every step of the movement by an amount proportional to the step size. However, because the integration is leaky, some small percentage of the value of the state variable is deducted in every step. The leaky integration model has two parameters: a gain k and a leak rate α. The gain describes how much distance a particular small movement (a single step, for example) adds to the state variable. The leak rate describes how much the state variable decays on every step. Mathematically, all of this can be formalized by the following differential equation:

$$\frac{\mathrm{d}p}{\mathrm{d}x} = -\alpha p + k, \qquad (1)$$

where $p(x)$ is the current perceptual position (i.e., the state variable), $\mathrm{d}x$ is the change of position of the participant along the trajectory of the movement, α is the rate of decay of the integrator, and k is the gain. In this equation, for each step $\mathrm{d}x$, the state variable p is reduced in proportion to its current value (due to the leak) and incremented by the distance given by the gain k of the step. The gain k, thus, influences the distance with which each individual step enters the integration. If $k = 1$, the visual motion is transformed perfectly into the instantaneous travel distance. If $k < 1$, the transformation underestimates the current step. If $k > 1$, the size of the current step is overestimated. The leak rate α influences how much of the integration is lost over a longer movement.

The integrated distance p for a true distance x is obtained by solving this equation. It is expressed as:

$$p(x) = \frac{k}{\alpha}(1 - \mathrm{e}^{-\alpha x}). \qquad (2)$$

If the leak rate α is large, then the perceived distance p of an extended movement is smaller than the true distance x, consistent with the experimentally observed underestimation of distance from the starting point (Frenz and Lappe 2005; Frenz et al. 2007; Lappe et al. 2007). The experimentally observed overestimation of distance traveled enroute to a goal is explained in the leaky integrator model by assuming that the state variable is the distance to the target, which has to be nulled by the movement (Mittelstaedt and Glasauer 1991; Lappe et al. 2007). In that case, the state variable is decremented for every step by an amount proportional to the length of the step size and the gain k. The leak α further reduces the value of the state variable such that the remaining distance to the goal is reduced by two processes in parallel: the decrement according to the movement and the leakage of the integrator.

The integration in Eq. 2 takes place over space, not over time. Therefore, the leak is accumulated while space is traversed, not while time passes. However, the leak might accumulate with walked distance or might accumulate according to the represented distance from the starting point. For movements along a straight line, these two possibilities cannot be distinguished, but for movements along a curvy path, the distance traveled along the path and the distance accumulated from the origin are distinct.

Consider movement along a path veering left and right of a straight line connecting the origin to the end of the movement. The length of the path increases with increasing amplitude of the sideways veering (Fig. 1) but the beeline distance between the start and the end of the movement remains fixed. Depending on how the leaky integration is performed, different outcomes of the integration can be conceived. First, curvilinear distance may be integrated along the length of the path. For each step along the path (black vector in Fig. 2a), the length of the step is added to the state variable with its gain k. Alternatively, distance along the route to the goal, i.e., along the origin-to-endpoint axis (thick red segment in Fig. 2a) may be integrated. In that case, only the projection of the step vector on the respective axis is added to the state variable, again with a respective gain k.

The outcomes of leaky integration in these cases are shown in Fig. 2b. Curvilinear integration along the path predicts that the state variable (perceived curvilinear distance along the path) should increase with path length, but should underestimate the true distance along the path more for larger path lengths (black curve in Fig. 2). The increasing underestimation is due to the increased leakage for longer paths.

The prediction for distance along the origin-to-endpoint axis is illustrated in Fig. 2b for three specific path lengths: 20, 30, and 40 m (black dots). For integration along the origin-to-endpoint distance, two possible scenarios must be considered. First, participants may simply integrate their distance along a line connecting the origin with the endpoint, irrespective of how they move along the path. In this case, the reported distance should be independent of the amplitude of the veering, i.e., all veering amplitudes should

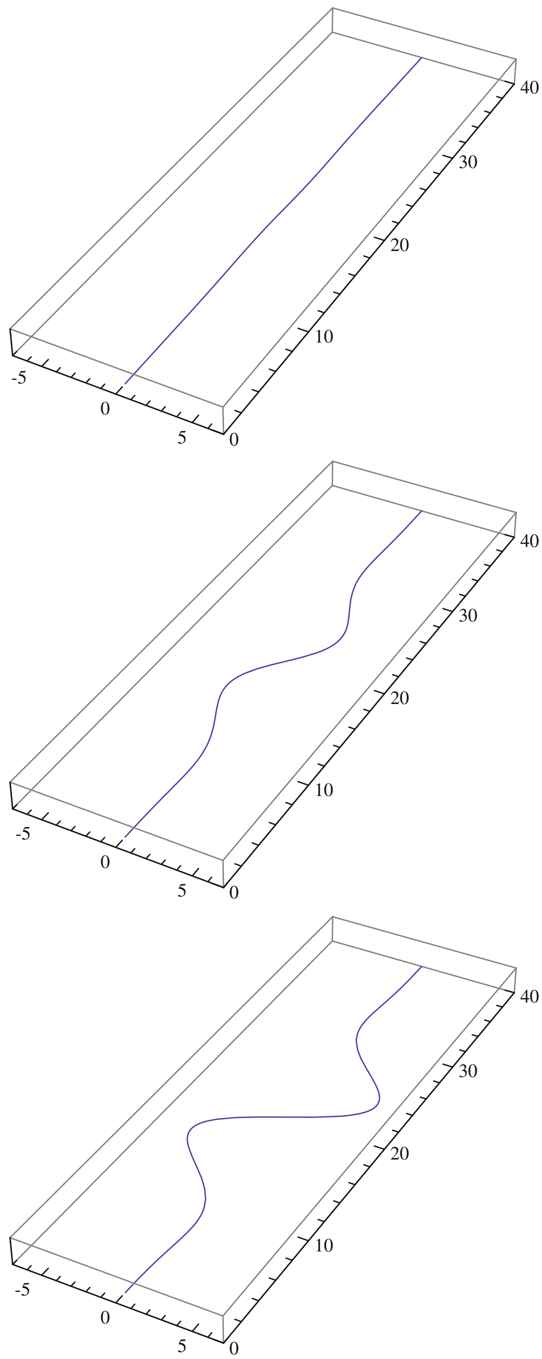

Fig. 1 Simulated movement from an origin to an endpoint along a trajectory that veered *left* or *right*. The trajectory followed a Gabor function with smooth increases and decreases of curvature at the origin and endpoint. Different amplitudes gave different increases in path length for the same origin-to-endpoint distance. *Top* almost straight path. *Middle* path length increase by 5%. *Bottom* path length increase by 20%. In the simulations, the viewing direction was always parallel to the origin-to-endpoint distance and did not vary with the instantaneous travel direction

give the same distance report for each of the three origin-to-endpoint distances. This possibility is shown in blue in Fig. 2b.

Second, participants may perform integration along the path but using the projection of the movement vector on the origin-to-endpoint axis, i.e., the component of the movement that is in the direction toward the endpoint. In this case, the state variable that is integrated would be the distance along the origin-to-endpoint line, the red segment in Fig. 2a, but the integration would run over the path segment, i.e., the black vector in Fig. 2a. Because the leak accumulates with the integration, the total amount of leakage would increase with increasing path length. Thus, the prediction from this possibility is that the reported distance from origin-to-endpoint for each of the three true distances should decrease rather than increase with increasing path length. This is shown in red in Fig. 2b.

In mathematical terms, the black curve gives the prediction if p and dx in Eq. 2 both run along the path, the blue curves give the prediction if p and dx both run along the origin-to-endpoint line, and the red curves give the prediction if p runs along the origin-to-endpoint line, but dx runs along the path. The three cases can be formalized as follows. If we denote the position along the curve with s and the distance along the curve with C, then the first case corresponds to

$$\frac{\mathrm{d}C}{\mathrm{d}s} = -\alpha C + k. \tag{3}$$

If we denote the position along the origin-to-endpoint line with x and the distance along the origin-to-endpoint line with D, then the second case corresponds to

$$\frac{\mathrm{d}D}{\mathrm{d}x} = -\alpha D + k. \tag{4}$$

The third case then corresponds to

$$\frac{\mathrm{d}D}{\mathrm{d}s} = -\alpha D + k. \tag{5}$$

To decide between these possibilities, we simulated movement along a path veering successively left and right of a straight line and asked observers to indicate the distance between origin and endpoint of the movement. By varying the amplitude of the veering, we created differences between the distance of the movement and the length of the path that was traversed and determined the influence of the path length on the distance judgment.

Methods

Participants

Thirteen participants (4 women, 9 men, between 22 and 41 years old) participated in the study after giving informed consent. All had normal or corrected-to-normal

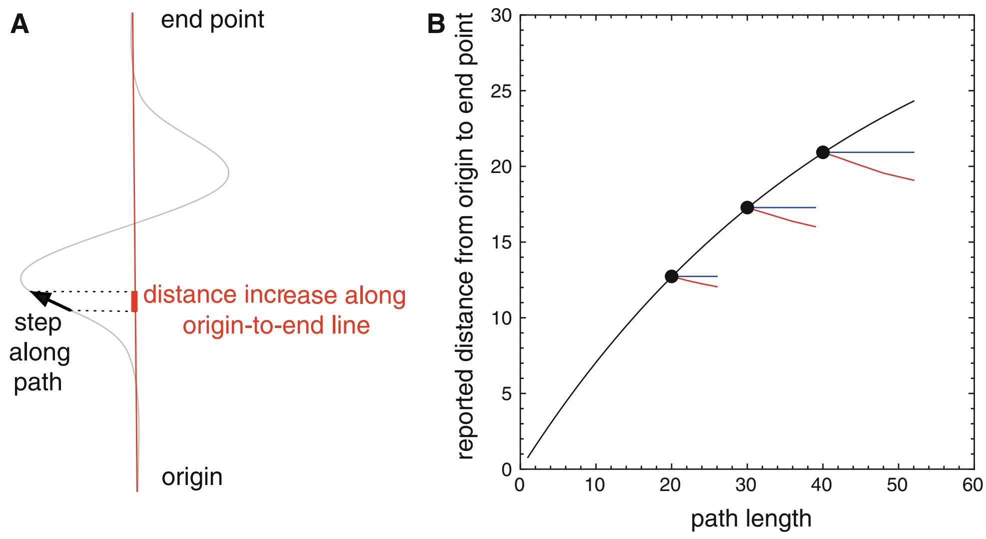

Fig. 2 State variable, integration procedures, and possible outcomes of the leaky path integration. **a** When moving along the *curved path*, each step along the path results in a distance increase along the origin-to-endpoint line. This increase is the projection of the step vector onto that line. Participants were asked to estimate their travel distance along this line. **b** Predicted results of three different possible integration procedures. See text for a detailed description

vision. They were members or students of the department. Students received course credit for participation.

Setup and stimuli

The participant stood 1.25 m in front of a 2.5 m wide and 2 m high projection screen in a dimly lit room. The field-of-view was 90 by 77° of visual angle. The visual stimulus was presented by an Electrohome ECP 4100 video projector running at 120 Hz frame rate with 1,280 × 1,024 pixel resolution. The stimulus simulated movement over a ground plane surface, similar to previous experiments (Frenz and Lappe 2005). The plane was mapped with a gravel texture. The texture of the surface was smoothed with a mip-mapping technique. The stimuli simulated movement along a 2D path veering left and right around the central forward direction (Fig. 1). The sideways path deviation was constructed as a Gabor function, i.e., a sine wave multiplied by a Gaussian,

$$S(x) = e^{-\frac{(x-\mu)^2}{2\sigma^2}} \times A \times \sin(\nu x - \Phi), \tag{6}$$

where x is the current position along the origin-to-endpoint axis. The Gabor function was chosen because it combines a smooth sideways back and forth veering from the sine wave with straight ahead movement at the start and end of the path provided by the increase and decrease of the Gaussian weighting. The frequency ν of the sine wave was $4\pi/D$, with D being the origin-to-end-point distance. Together with $\mu = D/2$ and $\sigma = D/7$, this gave essentially a single left/right deflection of the path (Fig. 1). The phase Φ was chosen randomly between 0 and 2 π to prevent the crossing of the path with the origin-to-endpoint axis from always being at $D/2$. The amplitude A was varied in order to obtain particular increases in path length, either 0, 5, 10, 20, or 30% increase with respect to the origin-to-endpoint distance. The velocity of the simulated movement along the path was adjusted according to the 2/3-Power-Law (Viviani and Stucchi 1992) to achieve a natural movement. The simulated facing direction was straight ahead and parallel to the origin-to-endpoint axis throughout the movement, to avoid interference of self-rotation with the perception of path curvature (Bertin et al. 2000). Control experiments in which the facing direction was always in the instantaneous direction of travel gave essentially the same results.

Design

A 3 × 5 × 3 design was used for the experiment. Three different origin-to-endpoint distances were used: 20 m, 30 m, and 40 m. This distance range was within the range that showed clear leakage effects in previous experiments. Five different path lengths were used, which were 0, 5, 10, 20, and 30% longer than the origin-to-end-point distance. Finally, three duration were used: 20, 30, and 40 s. The corresponding velocity for each trial was calculated according to the duration and distance of the trial and was close to those of human locomotion. Since we believe that path integration has evolved in the context of locomotion on foot, we wanted to test it in this speed range. In the experiment, each of the 45 conditions was presented once. The order of presentation was randomized.

Procedure

A single trial consisted of a movement simulation followed by the report of distance given by the participant. Participants were instructed to report the distance between the origin of the movement and the endpoint of the movement along a direct connecting line (beeline). They were told that the movement would veer sideways but that they had to monitor the distance along the straight line to the goal. Because the movement started and ended with linear segments (Fig. 1), participants had no problem in identifying the direction toward the goal.

Participants had to provide their distance estimate with two different reporting procedures. The first was an interval adjustment procedure similar to that used in earlier work (Frenz and Lappe 2005). Two horizontal lines appeared on the simulated ground plane after the simulated self-motion ceased. One of the lines was a reference line in a fixed distance of one eye height from the participant. The second line was adjustable and could be moved in depth across the ground plane with a computer mouse. Participants were instructed to adjust the second line such that the interval in depth along the ground plane between the two lines matched the origin-to-endpoint distance of the movement. The placement of the second line was recorded by the computer when the participant clicked the mouse button. Thereafter, participants had to provide a verbal estimate of the origin-to-endpoint distance. They were instructed to estimate the distance in meters as if they were physically standing on the ground plane. The verbal estimates were recorded by the experimenter.

Before data collection started, participants were allowed to familiarize themselves with the stimuli and the task. Initially, each participant saw an illustrative stimulus while the experimenter explained the task. The experimenter pointed out that each of the origin-to-endpoint distances that were used in the experiment could be represented with an interval on the displayed ground plane. Subsequently, it was checked whether the participant understood the adjustment of a perspective interval with the adjustment lines. Participants were requested to adjust a few intervals that were verbally specified by the experimenter. After each adjusted interval, they were also requested to adjust an interval that was twice as large.

Participants were then allowed to practice the main experimental task as much as they wanted. While doing so, they had to express the interval length verbally. There was no direct feedback by the experimenter, but if there were great differences between perspective interval adjustment and verbal report, the experimenter explained the perspective representation and procedure again, and participants continued to practice the adjustment procedure without feedback as long as they liked.

Results

All participants showed a systematic underestimation of travel distance as expected from previous studies (Frenz and Lappe 2005; Lappe et al. 2007). Underestimation occurred for both response types, interval adjustment, and verbal report, also consistent with previous results (Frenz et al. 2007). The two responses were well correlated in most participants. The correlation index, averaged over all participants, was 0.7. Three participants showed a weak correlation between the two response measures (correlation coefficient below 0.45) indicating that they were inconsistent in their response behavior. Those participants were removed from further analysis. However, we checked that the results reported in the following were not affected by the exclusion or inclusion of those participants. The average correlation coefficient of the remaining ten participants was 0.85. Because the correlation between the two responses was high but not perfect, we computed a composite measure, the mean of the two responses that resulted in some reduction in the noise of the responses. For each trial of every participant, the mean response, averaging the line placement response and the verbal response, was used in the subsequent analysis.

The leaky integrator model predicts that the perceived distance from the origin to the endpoint depends not only on the true distance from the origin to the endpoint but also on the length of the path that was traversed during the simulated movement. Moreover, the model predicts that the duration of the movement should not affect the outcome because the integration takes place over space, not over time. A three factor ANOVA on the response data with factor distance, path length, and duration gave a significant main effect of distance ($F_{8,2} = 19.04$, $P = 0.001$), a significant main effect of path length ($F_{6,4} = 11.17$, $P = 0.006$), no significant influence of duration ($F_{8,2} = 1.44$, $P = 0.29$), and no interaction between any of the factors. This is consistent with the predictions of the leaky integrator model.

The response data are shown in Fig. 3. The figure plots the reported distance between start and endpoint of the movement as a function of the length of the path that was traversed. The three different origin-to-endpoint distances (20, 30, and 40 m) are color coded. Blue data points correspond to 20 m, green data to 30 m, and magenta to 40 m. Each data point represents the average across participants for a particular origin-to-end-point distance and a particular path length. Data from the three durations for that simulated movement were collapsed for each participant. The range bars give the standard errors over participants.

The first data point for each origin-to-endpoint distance corresponds to the perceived distance along an almost straight path from the origin to the endpoint. The distance is clearly underestimated; 20 m distances are reported as 13, 30 m as 17 m, and 40 m as 22 m. Moreover, the underestimation increases with distance; the reported distances are 65, 57, and 55% of the true distances 20, 30, and 40 m. Both observations are consistent with leaky

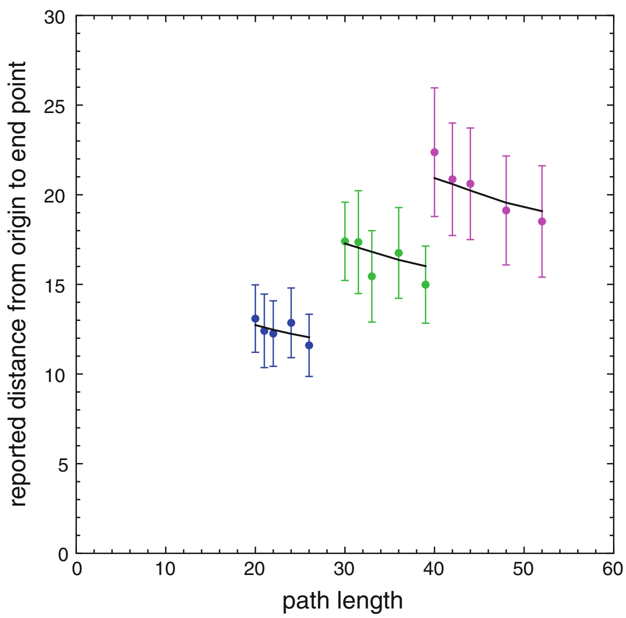

Fig. 3 Reported distance between the origin and the endpoint of the movement as a function of the length of the path that was traversed. Each point is the average across participants with standard errors indicated by the range *bars*. *Left* data points correspond to the five path lengths for an origin-to-endpoint distance of 20 m. *Central* data points correspond to the five path lengths for a origin-to-endpoint distance of 30 m. *Right* data points correspond to the five path lengths for a origin-to-endpoint distance of 40 m. The *black lines* are model fits of the data from the leaky integration model. All data have been fitted with a single parameter set. The best fitting parameters were $k = 0.785$ and $\alpha = 0.022$. The results clearly show that the perceived distance decreases with increasing path length as predicted by the leaky integration model

integration, which predicts that the leakage, and hence the underestimation, should increase with distance.

Comparison of the reported distances within each color-coded origin-to-endpoint distance shows the effect of the veering path and the corresponding increase in path length. For the 30 and 40 m origin-to-endpoint distance, the estimated origin-to-endpoint distance decreased as the path length increased (separate one way ANOVAs, $P < 0.05$). Thus, as the path that was traversed during the simulated movement grew longer, the perceived distance at the end of the movement grew smaller. For the 20 m distance, the decrease did not reach significance, but at these distance, any decrease would be expected to be small and, thus, less likely to attain statistical significance.

These decreases in perceived distance with increased path length are predicted by the leaky integration model if participants accumulated their distance from the origin of the movement, but did so with a leaky integration along the path that they traversed. We implemented this integration along the path in the leaky integrator model. We then determined the predicted perceived distances of each condition in the model. The results are shown by the black lines in Fig. 3. The integration was done numerically along each of the simulated paths. For this procedure, the path was split into many small segments or steps, and the numerical integration was done stepwise, beginning at the start point. For each step, we added its respective distance change along the origin-to-endpoint axis, i.e., the component of the path step vector parallel to the direction from the origin to the endpoint, with a gain factor k to the state variable. Then, we decreased the state variable in proportion to the step length (the norm of the vector) and the leak rate α. Thus, the state variable is the current origin-to-endpoint distance, but the amount of leak is tied to the path that is actually travelled. This leaky integration model was fitted to the data (black lines in Fig. 3). The best fitting parameters were $k = 0.785$ and $\alpha = 0.022$.

Discussion

Our participants experienced visually simulated self-motion along a sinusoidally veering path and were asked to indicate the beeline distance between the origin and the endpoint of the movement. By increasing the amplitude of the veering, we increased the total length of the path of the self-motion but kept constant the distance from the origin to the endpoint. Depending on how the participants integrate the movement, three possible integration procedures can be considered (Fig. 2). First, if the participants were to ignore the instruction to integrate the beeline, and instead were to integrate the length of the path, then the reported distance should increase with distance along the path. This was not the case. Thus, participants must have integrated the distance from the origin, as instructed. Second, if participants were to truly integrate their distance along a line connecting the origin with the endpoint, then the reported distance should be independent of the amplitude of the veering, i.e., all veering amplitudes should give the same distance report. This was also not the case, since the distance reports for a fixed origin-to-endpoint distance decreased with increasing path length. This decrease is consistent with the third possibility, namely that the integration takes place along the path but using the projection of the movement vector onto the origin-to-endpoint axis, i.,e. the component of the movement that is in the direction toward the endpoint. Only in this case would a leak occur that is related to the length of the path rather than to the distance from the origin. We thus conclude that our participants were capable of integrating the distance from the origin of their movement, even when traveling along a curvy path, and that this integration was leaky and took place along the path that was actually traversed.

Our results confirm that human path integration from visual motion is an integration over space, not over time.

The variation in the duration of the movement had no significant influence on the reported distance, similar to earlier studies (Lappe et al. 2007; Lappe and Frenz 2009). Path integration over space has several advantages over path integration over time. First, it is more directly related to the measure in question since the aim of path integration is to estimate a distance in space. For example, distance estimation from the step length and the number of steps during walking is more precise than the estimation of a temporal interval of the same duration (Durgin et al. 2009). Second, it is independent of the duration, and hence the speed, of the movement at least for the natural walking range of speeds that we used in this and earlier studies. Leaky integration over time would result in different distance estimates for different speeds of the movement. Third, leaky integration over time would also result in changes of the distance estimate if the movement is temporarily interrupted, for example during periods of rest. Although one can imagine a temporal integration which is paused when motion is absent, this would not be a simple integration over time but rather a more complicated integration that takes the movement state into account. Leaky integration over space would instead simply keep the value of the distance state variable and continue with that value once the movement resumes. However, since many types of memory decay over time, memory of the current integrated distance may decay during periods of disruption of a movement, but such a decay would not be caused by the integrator itself.

An overestimation of short distances together with an underestimation of long distances could alternatively be explained by a regression to the mean (Israël et al. 1997). The encoding error model of path integration from vestibular and somatic cues (Fujita et al. 1993; Loomis et al. 1999) includes such a regression to the mean instead of leaky integration. A Bayesian combination of distance estimates on a logarithmic scale with learned distance priors could lead to a regression to the mean in distance estimation data (Glasauer et al. 2009). Although a regression to the mean might be present in our data, it would not explain why the distance estimates depend on path length or why some participants show underestimation of distance throughout the test range. Moreover, regression to the mean cannot explain why in the studies of Lappe et al. (2007) and Lappe and Frenz (2009) the adjust-target condition led to an underestimation of travel distance, while the move-to-target condition gave an overestimation.

Although earlier work has shown that humans underestimate travel distances, the underestimation in the present study was particularly strong, such that the best fitting value for the gain was lower and that for the leak rate was higher than in previous studies. This stronger underestimation was not due to the use of verbal responses or the averaging between the verbal and the line adjustment responses. We analyzed the data separately for both reports and found similar underestimation in both cases. The misestimations of travel distance are quite variable between participants (Lappe et al. 2007; Lappe and Frenz 2009). Thus, the difference may be due to the different group of participants in the present study.

In a previous formulation of the leaky integrator model (Lappe et al. 2007; Lappe and Frenz 2009), the movement was along a straight line and the distance along the path coincided with the distance from the origin. The present experiments dissociated path length from distance from the origin in order to better specify and refine the model. The results showed that the leak is tied to the cumulated path length even when the distance from the origin is integrated. Therefore, the integration process is separable from the state variable. The leak, hence, occurs in the integration process that takes place over the traversed path. The leak in this integration then affects the final value of the state variable. It can do so for different state variables that may be integrated, such as the beeline distance, the distance along the path, or the distance to a goal.

The combination of the origin-to-endpoint distance as the state variable and the distance along the path as the integrator variable provides an important concept for path integration, namely that the state variable does not have to be identical to the integrator variable. Integration is a particular mechanism to accumulate data. Many kinds of data can be integrated. For example, one could integrate vestibular acceleration signals along the path to obtain velocity at the end of the path. The variable that is integrated and the path over which it is integrated do not have to be the same. This has also been indicated in the difference between the move-to-target and the adjust-target conditions in the previous descriptions of the leaky integrator model, where two different state variables have been used for the two conditions.

For the state variable in the model simulation, we used the projection of the origin-to-self distance onto a specific axis: the origin-to-endpoint line (Fig. 2a). Our assumption here is that for each step of the movement, the participant can calculate how far this step would advance his position along this imaginary line. To use this projection, and perform integration along this particular axis, participants need to know where they are going. Because the paths we used in the experiment followed a Gabor function; the initial and final parts of the movement were aligned with the origin-to-endpoint axis and served to indicate the integration axis to the participants. In natural situations, when movement is voluntary and goal-directed, the origin-to-endpoint axis is provided by the intended direction to the goal.

However, we might consider a different state variable to be used for the integration: the momentary origin-to-endpoint distance at each step of the movement. One may think of this as a rubber band that is attached to the start location and moves with the participant along the curved path, indicating for every step how much more the participant has been removed from the start location. This state variable has the advantage that the participant does not need to know the start-to-endpoint direction. It is thus a simpler computation. On the other hand, using the momentary origin-to-endpoint distance at each step as the state variable disregards information about the angle relative to the origin. Using the projection on the origin-to-endpoint line takes the angle into account, because it is part of the projection procedure. Thus, the projection on the origin-to-endpoint line is a valid 2D computation of the progress along this line. It uses both components of the movement, even if only one is updated as the state variable.

For the experiments of the present paper, both state variables give very similar results, because the momentary origin-to-endpoint distance and the component along the origin-to-endpoint axis differ only very slightly along much of the Gabor path that we have used. We simulated the model also with momentary origin-to-endpoint distance as state variable. The results are virtually indistinguishable from the results of Fig. 3. Again, the best fitting values were $\alpha = 0.022$ and $k = 0.785$.

Our experiments were performed with simulated self-motion in virtual reality. During real locomotion vestibular, somatosensory and motor efference copy signals are available in addition to visual information. Real walking replications of the path integration experiments of Lappe et al. (2007) gave similar underestimations of large travel distances, consistent with the leaky integration model (Lappe and Frenz 2009). However, walking without vision to a remembered target is quite accurate over distances up to 24 m (Elliott 1987; Rieser et al. 1990; Loomis et al. 1992). Lappe and Frenz (2009) suggested that different sensory modalities contribute with different gains k to the integration. In that case, the gain for somatosensory or vestibular estimation of step length may be higher than that for visual estimation. This is consistent with recent experiments that estimated the weight of such body cues in relation to vision on the estimation of travel distance (Campos et al. 2010). Alternatively, there might be different integrators for the different sensory modalities, each providing an independent estimate of travel distance.

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