

Path Complexity Does Not Impair Visual Path Integration

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Here an experiment studying the influence of path complexity on visual path integration is presented. Using a back-projection VR setup, subjects were passively transported along paths and were then asked to point to the origin of the path as fast and as accurate as possible. The complexity of the outbound paths was systematically varied by changing the number of path segments, while keeping constant overall length, overall turning angle, and turning direction. Surprisingly, results showed a decrease in response time as well as a slight increase in pointing accuracy with increasing path complexity, contradicting the predictions from common path integration models. The overall result from the present study is that path complexity does not negatively influence path integration abilities. If anything, subjects were faster and more accurate on more complex paths.

Keywords: Path integration, path complexity, optic flow, spatial cognition, point to origin.

Introduction

Together with landmark navigation, path integration is the most important means to keep track of position and orientation during travel. In contrast to

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landmark navigation, in which position and orientation are specified by recognizing known landmarks in the environment, in path integration this is achieved by integrating perceived ego-motion over time (e.g., Mittelstaedt & Mittelstaedt, 1980). Path integration provides metric information, that is, information about distances and directions, between the navigator and visited places in the environment. This information can, for example, be used to return to these places (homing). Path integration is a basic navigation mechanism that is widespread in the animal kingdom, and that has been found in insects (e.g., Müller & Wehner, 1988; Collett & Collett, 2000) birds (e.g., Collett & Collett, 1982; Regolin, Vallortigara, & Zanforlin, 1994), and mammals (e.g., Alyan & McNaughton, 1999; Gallistel, 1990; Loomis, Klatzky, Golledge, & Philbeck, 1999; Mittelstaedt & Mittelstaedt, 1980).

Mechanisms of Path Integration

The mechanisms underlying path integration have been extensively studied in insects. The desert ant (*Cataglyphis fortis*) and the honey bee (*Apis mellifera*), for example, are well known for their path integration abilities. During navigation, these animals update a so-called home-vector, that is, a representation of the nest's or hive's position, allowing them to directly head homewards after long winding excursions (Collett, Collett, & Wehner, 1999; Müller & Wehner, 1988; Wehner, Michel, & Antonsen, 1994). It is assumed that desert ants update their path integration vector using a polarization compass and ego-motion information obtained by counting steps. In honey bees, on the other hand, optic flow is used as the main cue for ego-motion. Independent of the specific ego-motion cues, it is assumed that path integration in insects is a continuous process, providing a home vector at all times.

In humans, path integration is often studied in so-called *homing* or triangle completion experiments, in which blindfolded subjects are led along two sides of a triangle, and are then asked to complete the triangle, that is, to return to the starting place (e.g., Loomis et al., 1993). In these experiments the contribution of kinesthetic and vestibular cues to path integration is studied while visual cues are excluded. According to results from triangle completion studies, Fujita, Klatzky, Loomis, and Golledge, (1993) have proposed the *encoding-error model* for path integration assuming that navigation and path integration rely on the following processes: (1) sensing, that is, the acquisition of self-motion information, (2) creating a trace of the route (route representation), (3) forming a survey representation of the route, (4) computing the desired trajectory based on the route or the survey representation, and (5) executing the trajectory (see also Loomis et al., 1993). According to the encoding-error model, a home vector is not available at all times, but is computed only if required. Systematic errors during path integration arise from processes concerned with sensing and encoding the outbound path, rather than from processes concerned with the computation of the home-vector or with its execution (see also Klatzky, Beall, Loomis, Golledge, & Philbeck, 1999).

Visual Path Integration

A number of recent studies that made use of virtual reality technology investigated whether visual cues alone can serve as sufficient ego-motion information for successful path integration and homing behavior (see Ellmore & McNaughton, 2004; Kearns, Warren, Duchon, & Tarr, 2002; Peruch, May, & Wartenberg, 1997; Riecke, Veen, & Bühlhoff, 2002; Ruddle, Payne, & Jones, 1998). The general procedure in these visual homing experiments was usually as follows: Participants were seated in front of a computer monitor or a (cylindrical) projection screen and were shown the visual projection of a travel along a path consisting of several segments through a virtual environment. This travel could either be a passive transportation or an active navigation that was controlled by the participants (e.g., with a joystick or with a keyboard). While subjects, for example, actively navigated through the corridors of a virtual building in experiments by Ruddle et al. (1998), subjects navigated through 3D fields of blobs, restricting visual cues to pure optic flow, in experiments by Riecke et al. (2002). At the end of the path, participants were then asked to either navigate back to the starting place or to indicate the direction of the starting point of the traveled path using some interaction device. As in the triangle completion experiments with blindfolded subjects, homing or path integration performance was analyzed by evaluating pointing accuracy and homing accuracy. The general finding of the mentioned studies was that visual cues or even optic flow alone is sufficient to solve homing tasks. While Peruch et al. (1997) reported less accurate homing performance with visual information alone than reported by Loomis et al. (1993) for blindfolded walking, comparable effects of increased undershooting at larger distances for translations have been reported in both situations. Kearns et al. (2002), compared path integration performance from optic flow alone with path integration from optic flow and body senses. Their results provide additional evidence for the notion that optic flow alone was sufficient to solve homing tasks. If, however, additional ego-motion information from body senses was available it appeared dominant.

Path Integration and Path Complexity

Both, in blindfolded walking and visual path integration, only few studies have addressed the influence of path complexity on path integration. Using a homing task with blindfolded subjects, Klatzky et al. (1990), for example, compared subjects' homing accuracy after being led along paths consisting of one to three segments. They found increasing turn and distance errors with increasing path complexity which, for polygonal trajectories, was defined as the number of straight line segments. Similar results have also been found in other studies in which participants were either led along or actively navigated paths with differing number of segments (usually 2-4). At the end of the paths, participants were asked to navigate back to the starting point (Loomis et al., 1993), to indicate the direction to the starting point (Ruddle et al., 1998; Scholl, 1989), or to indicate the direction to objects within the environment (Rieser & Rider, 1991). The general outcome of these experiments was that pointing accuracy or

homing performance decreased with increasing number of segments of the paths. It is, however, important to note that in all these experiments the number of segments of the paths was confounded with both, overall path length and overall turning angle, that is, paths with 2 segments were shorter and required less turning than paths with more segments. The reported effects can, therefore, not be clearly attributed to the increase of path complexity.

In a blindfolded walking study, Loomis et al. (1993) used a subset of the paths used by Klatzky et al. (1990). In addition to the homing task, subjects had to retrace the paths after being led along the routes. Also retrace errors, that is, distances between retrace endpoints and correct locations, increased with increasing path complexity. While the latencies to begin the retrace were constant between path of different complexity, subjects showed an increased latency to start homing as path complexity increased. Vidal, Amorim, & Berthoz (2004) tested subjects' performance in recognizing virtual three-dimensional corridors after passive exploration. The corridors were composed of three to five segments. After exploration, subjects had to select from among four external views the corridor that corresponded to the one previously explored. Subjects' recognition accuracy decreased with increasing path complexity and recognition latencies increased. Note, however, that in the retrace task as well as in the recognition task in the latter two studies, subjects had to remember the traveled path in order to solve the tasks. Thus, these tasks differ from pure path integration or homing tasks where no memory of the traveled path is required.

Motivation and Hypotheses

This study investigates the influence of path complexity, that is, the number of straight-line segments of the outbound path, on visual path integration performance. While earlier studies have already addressed this issue, path complexity in these studies was confounded with further properties of the outbound paths such as path length and overall turning angle. In this study the complexity of the outbound path was separated from other path properties by systematically varying the path's number of segments, while keeping constant overall path length, overall turning angle, and turning direction.

Systematically varying the complexity of the outbound paths, also allows for the investigation of the mechanisms underlying human path integration, as the proposed path integration mechanisms (see above) predict different outcomes:

- **Continuous Updating:** In a continuous updating process the number of computation steps depends on the cycle time of the process, but not on the existence and number of straight line segments in the path. The accuracy of path integration should therefore be independent of the complexity of the path, but should solely depend on traveled distance and turning angle. Also, response times should be unaffected by path complexity as path integration is done online, that is, a home-vector is available at all times (for a recent overview on continuous path integration models, see Merkle, Rost & Alt, 2006).

- **Encoding-error Model:** The encoding-error model assumes that the traveled path is divided into straight line segments which are remembered. A home-vector is computed only if required, that is, it is computed offline. An increase in the number of segments along an outbound path should increase the difficulty of the task, as (i) memory demands for the route representation increase and (ii) as an increased route complexity should lead to an increase in computation load and processing time and to a decrease in path integration accuracy as computation errors add up.

Material and Methods

Participants

Eighteen subjects (9 female and 9 male subjects) participated in the experiment. They were mostly university students and were paid 8 Euro an hour.

Experimental Setup

Subjects were seated at a chair in front of a projection screen, such that their line of sight was centered on the screen covering 90° horizontal and 60° vertical field of view. The visual scenery was rendered on a standard PC running a C++ simulation software that was designed and programmed especially for psychophysical virtual reality experiments (<http://velib.kyb.mpg.de/>). The computer generated images were rendered with approximately 100 Hz, a resolution of 1280×1024 pixel, and a graphical field of view of $90^\circ \times 60^\circ$ and were projected onto the screen from behind. A small desk on which a standard joystick was mounted was placed directly in front of the subjects (see Figure 1).

The Virtual Environment

The experiment was performed in a virtual environment that consisted of a textured ground plane only. The texture of the ground plane was designed to create a convincing feeling of self-motion by optic flow, while no repetitive patterns were obvious that could have served as landmarks during the experiment.

Experimental Procedure

During each of three experimental phases, the introduction-phase, the training-phase, and the test-phase, subjects were passively transported along several paths consisting of multiple segments (see Figure 2). At the end of each path the message 'Point Now!' appeared on the screen, and subjects had to indicate the direction to the origin of the path as fast and as accurate as possible by moving the joystick into the corresponding direction. Pointing direction and response times were recorded for every trial.

During the introduction-phase, subjects were transported along 6 paths consisting of 2 to 5 segments. During navigation an arrow was shown in the

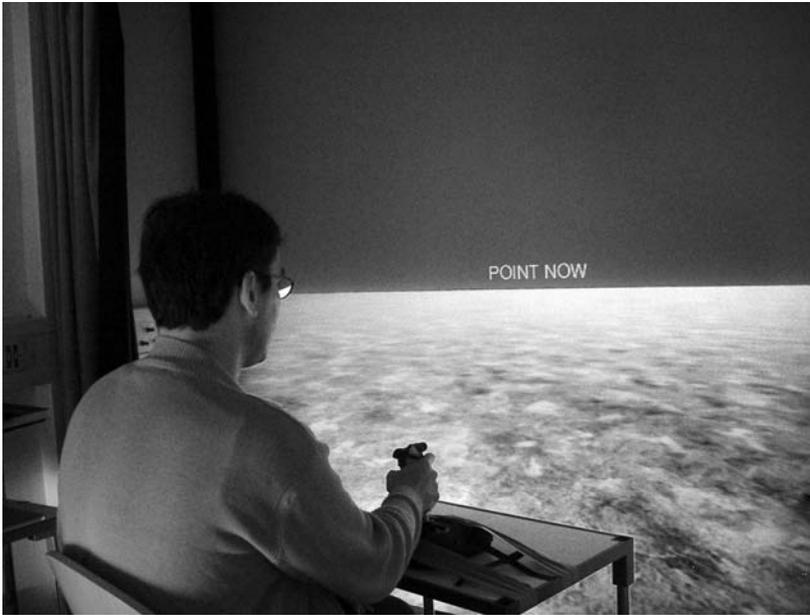


Figure 1. Experimental setup.

lower frontal field of view. This arrow always pointed to the origin of the path, thus helping participants to familiarize with the task.

During the training-phase subjects were transported along 8 paths consisting of 2–5 segments. The arrow was not visible during navigation. However, after

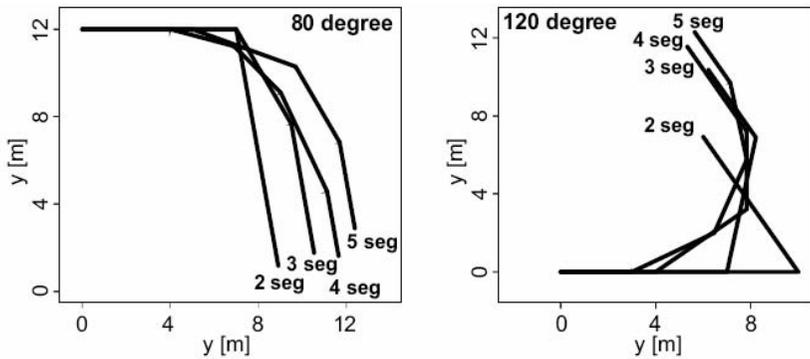


Figure 2. Example paths for the 80 degree right turn condition (left) and the 120 degree left turn condition (right).

subjects gave their direction judgments the arrow was shown for three seconds, indicating the correct direction from the endpoint of the outbound path towards the origin. The paths that were used during the introduction- and training-phase had overall turning angles between 50° and 150° and were different from the paths used in the test-phase.

During the test-phase subjects were passively transported along 48 paths. No arrow was present during navigation and no feedback was given. The overall turning angles of the paths were 40° , 60° , 80° , 100° , 120° , and 140° . For each of these turning angles 8 paths consisting of 2, 3, 4, and 5 segments were generated, half of which had right turns only and half of which had left turns only. Each path had an overall length of 18m, single segments had a minimum length of 3m and a maximum length of 12m. Between two subsequent segments turning angles between 10° and 140° were allowed. Figure 2 displays example paths for the 80° and the 120° condition. The 48 paths were presented in random order.

During passive transportation, translations and rotations were carried out successively and followed the same predefined trapezoid velocity profile with a linear velocity increase and a linear velocity decrease. Maximal translation speed was 2m/sec and maximal rotation speed was 25° /sec and was reached after .67 secs. The duration of the plateau of the trapezoid changed according to the length of the translation or rotation angle, respectively. Translations and rotations were clearly separated from each other. As subjects came to a complete stop at each segment transition, the different path segments were easily detectable.

Analysis

For the analysis of systematic pointing errors, the data were first normalized, that is, the target direction of all paths was set to 0° and subjects' direction judgments were adjusted accordingly. Furthermore, direction judgments of left-turn paths were mirrored, such that responses of left- and right-turn paths were directly comparable.

Results

Absolute Pointing Error

An ANOVA (number of segments, turning angle, Number of Segments \times Turning Angle) revealed significant main effects of the number of segments ($F = 5.32$, $df = 3$, $p < .01$) and the turning angle ($F = 3.17$, $df = 5$, $p = .01$) as well as a significant interaction ($F = 2.91$, $df = 15$, $p < .001$, see Figures 3 and 4). While no significant overall correlation was found between subjects' pointing error and the number of segments ($r = -.10$, $p = .4$), subjects' pointing error for 2 segment paths was significantly larger than the averaged pointing error of the 3, 4, and 5 segment paths (2 segment path: 31.09 ± 4.07 , 3–5 segments: 25.09 ± 4.23 , t test: $t = 2.95$, $df = 17$, $p < .01$). It is therefore likely

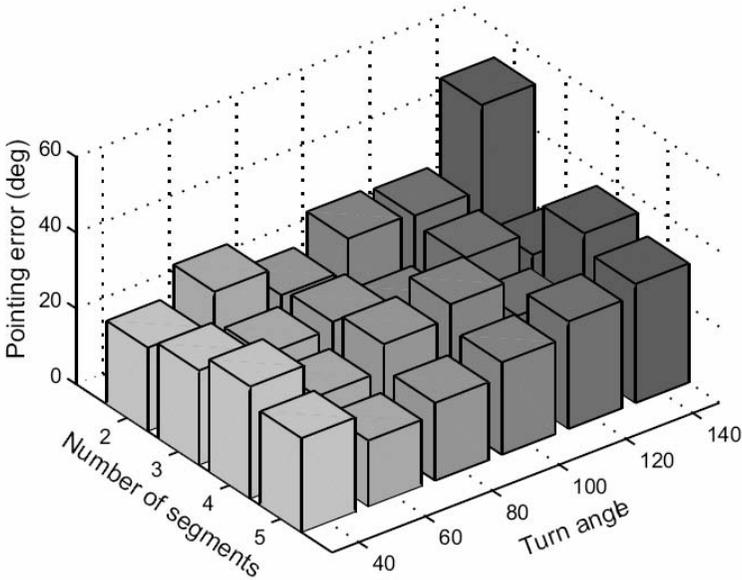


Figure 3. Subjects' absolute pointing error depending on path complexity (number of segments) and on the overall turning angle.

that the described effects can be mainly attributed to paths consisting of 2 segments with a 140° turning angle (see Figure 3). A re-analysis of the data in which these paths (140° turn angle, 2 segments) were omitted confirmed this

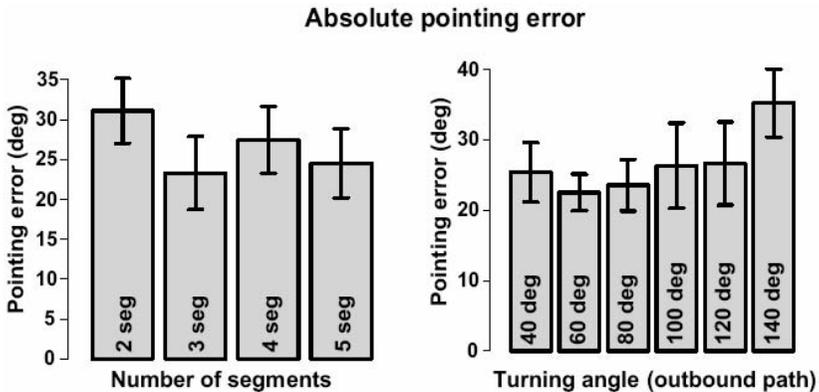


Figure 4. Absolute pointing errors for paths of different complexity (left) and for the different turn angles (right).

assumption: no significant main effects of either number of segments ($F = 1.82$, $df = 3$, $p = .15$) nor of turning angle ($F = .96$, $df = 5$, $p = .45$) were found. The interaction, however, remained significant ($F = 2.02$, $df = 14$, $p = .02$).

Differences in absolute pointing errors between female and male subjects did not reach statistical significance (females: 33.96 ± 7.29 , males: 19.21 ± 2.14 , t test: $t = 9.37$, $df = 14$, $p = .08$).

Response Time

An ANOVA (number of segments, turning angle, Number of Segments \times Turning Angle) revealed a main effect of the number of segments ($F = 5.42$, $df = 3$, $p < .01$), while no main effect of turning angle ($F = 1.94$, $df = 5$, $p = .10$) and no interaction was found ($F = 1.26$, $df = 15$, $p = .34$, see Figure 5). A paired t -test reveals a significant difference between the averaged response times of path with 2 and 3 segments and paths with 4 and 5 segments (average 2+3 segments: $2.59 \pm .31$ secs, average 4+5 segments: $2.17 \pm .30$, t test: $t = 3.6$, $df = 17$, $p < .001$).

A re-analysis of the data in which 2 segment paths with a 140° turn angle were omitted showed a significant main effect of the number of segments ($F = 4.5$, $df = 3$, $p < .01$), while neither a main effect of turning angle ($F = 1.0$, $df = 5$, $p = .41$) nor an interaction ($F = 1.0$, $df = 14$, $p = .45$) was found.

Female and male subjects did not differ in their average response times (female: $2.17 \pm .36$ sec, males: $2.58 \pm .51$ secs, t test: $t = 0.66$, $df = 14$, $p = .52$).

Systematic Pointing Error

Subjects' pointing performance was characterized by an overall tendency to undershoot if large turning angles were required and a systematic overshoot if small turning angles were required (see Figure 6 and Figure 7; note that on

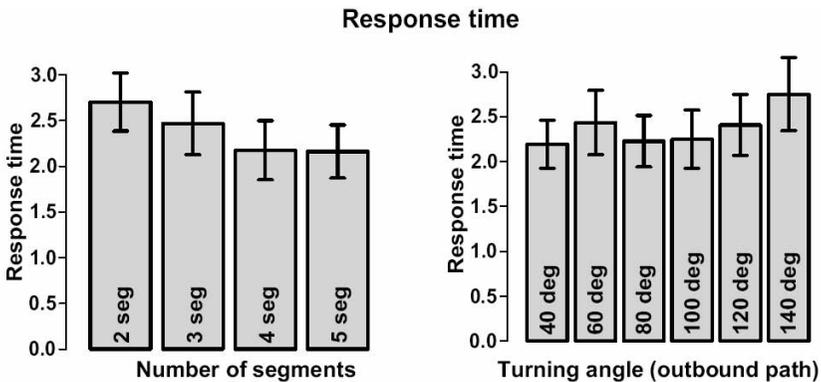


Figure 5. Response times for paths of different complexity (left) and for the different turn angles (right).

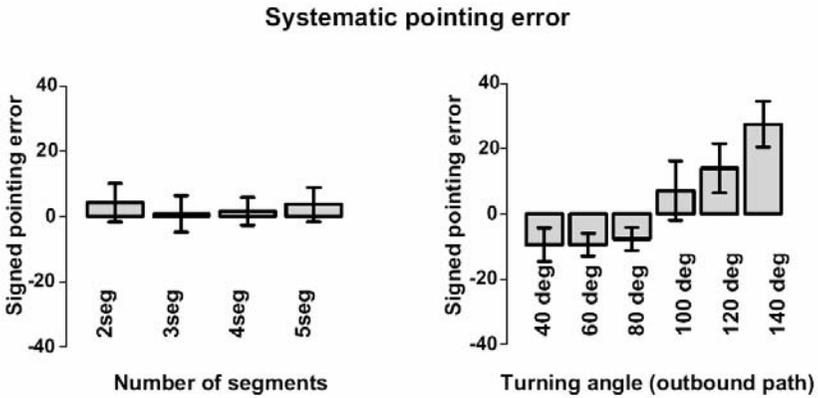


Figure 6. Systematic pointing errors for paths of different complexity (left) and for the different turn angles (right): positive values indicate a systematic overshoot, negative values indicate a systematic undershoot.

outbound paths with small overall turning angles [e.g., 40° and 60°], large turning angles were required in order to point homeward, and vice versa). An ANOVA (number of segments, turning angle, Number of Segments × Turning Angle) revealed a highly significant main effect of the turning angle of the outbound paths on the signed pointing error ($F = 23.17$, $df = 5$, $p < .001$). This

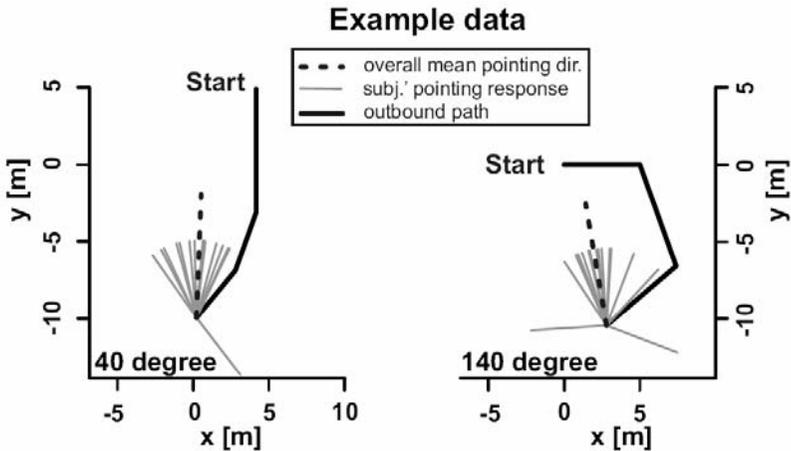


Figure 7. Example data for 2 paths consisting of 3 segments with 40° turning angle (left) and 140° turning angle (right), subjects' pointing responses are displayed by grey lines, the mean pointing direction is represented by the dashed line.

trend to produce prototypical responses has been termed 'compression of response range' and is known from triangle completion experiments with blindfolded subjects (e.g., Fujita et al., 1993). The number of segments of the outbound paths did not have an effect on systematic pointing error ($F = .87$, $df = 3$, $p = .46$), the interaction was significant ($F = 1.94$, $df = 15$, $p = .02$).

Correlation Between Response Time and Pointing Accuracy

No significant correlation was found between subjects' mean pointing accuracy (mean absolute pointing error) and subjects' mean response time on the group level ($r = .27$, $p = .29$). Correlations between pointing accuracy and response times were also calculated for each subject. Only for two subjects significant correlations were found, one of which was positive ($r = .32$, $p = .03$), and one of which was negative ($r = -.29$, $p = .05$). It can therefore be assumed that no apparent overall relation exists between response time and pointing accuracy in this experiment.

Discussion

The experiment studied the influence of path complexity on visual path integration by means of a speeded point-to-origin task. Path complexity was systematically varied by changing the number of segments of the paths while overall path length and overall turning angle were held constant between paths of different complexity. The experiment revealed several effects: Both pointing accuracy and response times were influenced by path complexity. The absolute pointing error was largest for the most simple paths, that is, on paths consisting of 2 segments only. Also, subjects' response time decreased with increasing path complexity. Subjects' systematic pointing error, however, was not influenced by path complexity, that is, subjects did not produce systematic underestimations or overestimations depending on the number of segments of the outbound paths. Subjects' pointing error also depended on the overall turning angle. The absolute pointing error was largest for the largest turn angle of 140° , while response time was independent of the overall turning angle. Furthermore, subjects' pointing responses undershot when a large pointing angle was required, that is, for paths with a small overall turning angle, and subjects' pointing responses overshot when a small pointing angle was required. This effect is in line with earlier studies and has been termed 'compression of response range' (see e.g., Loomis et al., 1993).

The results from this study are not in line with any of the two path integration mechanisms discussed in Motivation and Hypotheses section of the Introduction. The decrease of response time and pointing accuracy with increasing path complexity was neither predicted by a continuous updating process nor by the encoding-error model. If path integration was a continuous process, a home vector should be available at all times. Thus, response times should be independent of path complexity and pointing accuracy should solely depend on traveled distance and overall turning angle, but not on path

complexity. The encoding error model, on the other hand, suggesting that the traveled path is remembered and a home vector is computed only if required, predicts that both computation time, and therefore response time, as well as pointing error should increase with increasing path complexity.

It is important to note, however, that subjects' pointing performance was dramatically reduced with respect to average performance in one particular situation: on paths with 140° turning angle and 2 segments (see Figure 3). On these paths, subjects experienced a single turn with a 140° angle. It seems that, at least with the current experimental setup, such large turns are difficult to be perceived and/or to be integrated correctly. A re-analysis of the data in which these path (140° turning angle, 2 segments) were omitted, did no longer reveal a significant effect of path complexity on pointing accuracy. This latter result suggests that path integration performance is generally independent of path complexity, as postulated by a continuous updating process, if overall path length and overall turning angle are controlled for. However, even with the 140° turning angle and 2 segment paths omitted, a decrease in response time with increasing path complexity was apparent which can not be explained by a continuous updating process and which contradicts the encoding-error model. A possible explanation for this latter effect is a strategy shift between paths of different complexity. On simple paths, consisting of few segments only, subjects can easily remember the traveled path and compute a home-vector only if required, as suggested by the encoding-error model. If, however, paths are more complex, remembering the paths becomes too challenging. Thus, relying on a continuous updating process could be a reasonable strategy and would explain the decrease in response time. This explanation is supported by informal interview with several subjects.

Taken together, results from the present study demonstrate that path complexity does not negatively influence path integration abilities. If anything, subjects were faster and more accurate on more complex paths. While this result seems surprising at first glance, one has to take into account that the paths humans navigate in everyday life are far more complex than the paths usually used in triangle completion tasks and more complex than even the most complex paths of this study. If path integration abilities were negatively influenced by path complexity, the path integration system would not make any useful contribution to everyday navigation. One might argue that path integration mechanisms assuming that traveled paths are divided into discrete straight line segments, such as the encoding-error model (cf. Fujita et al., 1993; Loomis et al., 1993; Klatzky et al., 1999), are not generally plausible. First, because it is not clear how such segments are defined when navigating natural trajectories, and second, because these mechanisms would not make any predictions for curved trajectories. Furthermore, it is suggested that the concept of path complexity as defined by the number of line segments is conceptually flawed for several reasons: First, here we showed that increasing path complexity did not result in decreased path integration performance. Second, as shown in Figure 2, paths differing largely in complexity may be almost indistinguishable when

sketched out on paper. Third, as stated above, natural paths can hardly ever be decomposed into a small number of straight lines. The number of segments definition, however, applies only to such polygonal paths. It therefore appears to be necessary to study path integration abilities and the underlying mechanisms in experiments with more natural paths, that is, with long and curved paths.

References

- Alyan, S., & McNaughton, B. L. (1999). Hippocampectomized rats are capable of homing by path integration. *Behavioral Neuroscience*, *113*, 19–31.
- Collett, M., & Collett, T. S. (1982). Do geese use path integration for walking? In F. Papi & H. Wallraff, *Avian navigation* (pp. 198–307). Berlin: Springer.
- Collett, M., & Collett, T. S. (2000). How do insects use path integration for their navigation. *Biological Cybernetics*, *83*, 245–259.
- Collett, M., Collett, T. S., & Wehner, R. (1999). Calibration of vector navigation in desert ants. *Current Biology*, *9*, 1031–1034.
- Ellmore, T. M., & McNaughton, B. L. (2004). Human path integration by optic flow. *Spatial Cognition and Computation*, *4*, 255–272.
- Fujita, N., Klatzky, R. L., Loomis, J. M., & Golledge, R. G. (1993). The encoding-error model of pathway completion without vision. *Geographical Analysis*, *25*, 295–314.
- Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT Press, Bradford Books.
- Kearns, M., Warren, W., Duchon, A., & Tarr, M. (2002). Path integration from optic flow and body senses in a homing task. *Perception*, *31*, 349–374.
- Klatzky, R. L., Beall, A. C., Loomis, J. M., Golledge, R. G., & Phillbeck, J. W. (1999). Human navigation ability: Tests of the encoding-error model of path integration. *Spatial Cognition and Computation*, *1*, 31–65.
- Klatzky, R. L., Loomis, J. M., Golledge, R. G., Cicinelli, J. G., Doherty, S., & Pellegrino, J. W. (1990). Acquisition of route and survey knowledge in the absence of vision. *Journal of Motor Behavior*, *22*, 19–43.
- Loomis, J. M., Klatzky, R. L., Golledge, R. G., Cicinelli, J. G., Pellegrino, J. W., & Fry, P. A. (1993). Nonvisual navigation by blind and sighted: Assessment of path integration ability. *Journal of Experimental Psychology: General*, *122*, 73–91.
- Loomis, J. M., Klatzky, R. L., Golledge, R. G., & Philbeck, J. W. (1999). Human navigation by path integration. In R. Golledge (Ed.), *Wayfinding behavior* (125–152). Baltimore: Johns Hopkins University Press.
- Merkle, T., Rost, M., & Alt, W. (2006). Egocentric path integration models and their application to desert arthropods. *Journal of Theoretical Biology*, *240*, 385–399.
- Mittelstaedt, M. L., & Mittelstaedt, H. (1980). Homing by path integration in a mammal. *Naturwissenschaften*, *67*, 566–567.
- Müller, M., & Wehner, R. (1988). Path integration in desert ants, *Cataglyphis fortis*. *Proceedings of the National Academy of Sciences*, *85*, 5287–5290.

- Peruch, P., May, M., & Wartenberg, F. (1997). Homing in a virtual environment: Effects of field of view and path layout. *Perception, 26*, 301–311.
- Regolin, L., Vallortigara, G., & Zanforlin, M. (1994). Object and spatial representations in detour problems by chicks. *Animal Behavior, 49*, 195–199.
- Riecke, B. E., van Veen, H. A. H. C., & Bühlhoff, H. H. (2002). Visual homing is possible without landmarks: A path integration study in virtual reality. *Presence - Teleoperators and Virtual Environments, 11*(5), 443–473.
- Rieser, J., & Rider, E. (1991). Young children's spatial orientation with respect to multiple targets when walking without vision. *Developmental Psychology, 27*, 97–107.
- Ruddle, R. A., Payne, S. J., & Jones, D. M. (1998). Navigating large scale "desktop" virtual buildings: Effects of orientation aids and familiarity. *Presence: Teleoperators and Virtual Environments, 7*, 179–192.
- Scholl, M. (1989). The relation between horizontality and rod-and-frame and vestibular navigational performance. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 15*, 110–125.
- Vidal, M., Amorim, M.-A., & Berthoz, A. (2004). Navigating in a virtual three-dimensional maze: how do egocentric and allocentric reference frames interact? *Cognitive Brain Research, 19*, 244–258.
- Wehner, R., Michel, B., & Antonsen, P. (1994). The hidden spiral: Systematic search and path integration in desert ants, *Cataglyphis Fortis*. *Journal of Comparative Physiology, 175*, 525–530.