Human navigation ability: Tests of the encoding-error model of path integration

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Abstract. This paper tests the generality and implications of an "encoding-error" model (Fujita et al. 1993) of humans' ability to keep track of their position in space in the absence of visual cues (i.e., by nonvisual path integration). The model proposes that when people undergo nonvisually guided travel, they encode the distances and turns that they experience, and their errors reflect systematic inaccuracies in the encoding process. Thus when people try to return to the origin of travel, they base their response on mis-encoded values of the outbound distances and turns. The two experiments reported here addressed three issues related to the model: (i) whether path integration is context-dependent and if so, how rapidly it adapts to recently experienced distances and turns; (ii) whether effects of experience can be specifically attributed to changes in the encoding process, and if so, what changes; and (iii) whether the encoding process represents distances and turns in the individual paths without considering their spatial relationship to one another (i.e., an object-centered representation). Testing these issues allows us to evaluate and develop the model.

Subjects who were blindfolded or had restricted vision were led through two legs of a triangle and the turn between, then tried to return to the origin. Paths varied in whether experienced legs and turns were small or large (Experiment 1) and in variability of return and outbound course (Experiment 2). Response turn, distance and course were determined. The assumption of immutable encoding functions was not supported; encoding processes were context dependent, although they did not adapt within a block of trials. Although effects of experience could be accounted for by the model, the affected parameters were not always as predicted, and in some cases additional parameters were necessary. Results of manipulating variability in return course were consistent with the model's assumption of object-centered representation.

Key words: blind, encoding, human navigation, path integration

Path integration and the return-to-origin task

An emerging view of navigation in humans and other species is that there are two distinct means of keeping track of position and orientation during travel:

landmark-based navigation and path integration (for a general reference, see Gallistel 1990). In the first case, landmarks provide the traveler with direct sensory information about current position and orientation. With path integration, the traveler uses sensed self-velocity or self-acceleration to update current position and orientation relative to some starting point. Our concern in this paper, as in our earlier work (Fujita et al. 1993, 1990; Klatzky et al. 1995, 1990; Loomis et al. 1993), is with human path integration based solely on proprioceptive and vestibular cues. We have focused on these idiothetic (internal) inputs to the exclusion of allothetic (external) inputs like optic flow, acoustic flow, and azimuthal information because of our interest in the ability of blind and blindfolded sighted observers to perform path integration without external reference.

A prototypical task for studying path integration is that of traveling from an origin along an outbound path of varying direction and then, at some point on the path, attempting to return directly to the origin. A wide variety of animal species have exhibited an impressive level of accuracy at returning to the origin of travel solely on the basis of path integration. A sizable number of studies of human path integration without sight have also been conducted using either this return-to-origin task or alternatively, a point-to-origin task (Beritoff 1965; Juurma and Suonio 1975; Klatzky et al. 1990; Landau et al. 1984; Loomis et al. 1993; Rieser and Frymire 1995; Mittelstaedt and Glasauer 1991; Sauve 1989; Sholl 1989; Worchel 1951, 1952; Yamamoto 1991). Human performance is generally poorer than that of these other species. However, in the non-human studies, the animals actively traversed the outbound path, optic flow information was often available for sensing velocity, and an allothetic azimuthal reference was sometimes present, whereas in the human studies, subjects were passively guided along the outbound path, no visual information was available, and there was no azimuthal reference. It should also be noted that several lower species have been found to exhibit systematic errors even in the presence of azimuthal cues (see Maurer and Séguinot 1995).

An organism performing this task might, at a minimum, simply maintain a representation of current orientation and position, the latter being in the form of Cartesian coordinates along some cardinal axes (Mittelstaedt 1985) or in the form of polar coordinates specifying the distance and direction to the origin (Fujita et al. 1990; Gallistel 1990; Müller and Wehner 1988). Updating of the representation would occur moment-by-moment (e.g., step-by-step) with only current position and orientation being stored in memory (see Benhamou and Ségunoit 1995; Maurer and Ségunoit 1995). An alternative to the moment-by-moment model, which we call a configural model, assumes that the entire outbound trajectory is stored in memory and that when

the organism wishes to return to the origin, it uses this stored configuration to compute the bearing to the origin. Whereas moment-by-moment models appear to apply to many animal species, the model of human path integration investigated here, called the encoding-error model, is a configural model.

Assumptions of the encoding-error model

A general characterization of human path integration assumes that it depends upon a number of sub-processes (see also Loomis et al. 1993; Fujita et al. 1993). These sub-processes are (i) sensing the outbound path, (ii) forming a representation, either of the path or of current position and orientation, (iii) computing a return path, and (iv) executing that path. Taken together, the first two sub-processes, which culminate with an internal representation suitable for initiating the return, are referred to as "encoding". The encoding-error model proposes that systematic errors in path integration reflect systematic inaccuracies in the encoding process, and not in the processes of computing and executing the return path. Thus errors in the turn and distance people execute when trying to return to the origin of travel are due to mis-representation of the outbound distances and turns.

We focus on the encoding-error model in the present paper, to the exclusion of others (see, e.g., Maurer and Séguinot 1995), because of its excellent fit to an extensive investigation of human path integration ability, reported by Loomis et al. (1993). That investigation was part of a larger study of spatial ability by blind and blindfolded, sighted subjects (see also Klatzky, et al. 1995). In the primary return-to-origin task of the study, subjects were passively guided along two legs of a triangle (Leg-A and Leg-B) with a turn in between (Turn-1); upon reaching the end of the second leg, subjects attempted to return unaided to the origin. The response measures were the turn made by the subject back toward the origin (Turn-2) and the distance subsequently walked (Leg-C). Because subjects were passively guided along the outbound path but generated and actively controlled their attempted return to the origin, we assume that the sub-processes were different for the two portions of the task: (a) sensing and building a representation of the outbound portion and (b) computing and executing the return portion.

Twenty-seven triangular pathways were completed by each subject, representing factorial combinations of three values of Leg-A length, three of Leg-B length (in both cases 2, 4, and 6 m), and three values of Turn-1 (60 deg, 90 deg, and 120 deg). When the mean response values were plotted as a function of the correct values, the data exhibited a very systematic pattern. Each function was essentially linear with a slope less than 1 and a positive zero-intercept, and it tended to cross the diagonal near the mean. As a result, the

range of responses was considerably reduced relative to the range of correct values, and there was over-responding at the low end of the response range and under-responding at the high end, with the highest accuracy for responses near the mean of correct values.

The encoding-error model was subsequently developed and fit to these data by Fujita et al. (1993). The data tested the assumption that the systematic error pattern observed in the data can entirely be attributed to errors made at the encoding stages of navigation, those culminating in a representation suitable for return to the origin. Recall that six stimulus values – 3 leg lengths and 3 turn angles – were used to construct the pathways used by Loomis et al. (1993). The model assumed that there was an encoded value corresponding to each of those stimulus values. Given the encoded values for a particular outbound path, the navigator presumably computed the return path accurately and executed the response accurately (or with only nonsystematic error), ending at some stopping point. Errors in encoding, then, produced systematic departures of those stopping points from the actual origin of the pathway.

The encoded values for each of the six stimulus values were estimated by minimizing the distance between the model-predicted stopping points of the subjects and the empirically determined ones. When the estimated encoded values were plotted against the actual stimulus values for leg length and turn, the resulting functions proved to be highly linear. The linear encoding functions resulted in an encoding model of only four parameters – the slope and intercept of the function relating encoded distance to actual distance (estimated to be 0.60 and 1.2 m, respectively), and the slope and intercept of the function relating encoded turn to actual turn (estimated to be 0.48 and 44°).[1] These four parameters indicate that the mean of presented values was encoded accurately, but low values were overestimated and high ones underestimated, constituting regression to the mean in encoding. The model provided an excellent fit to the data.

The goodness of fit means that path integration in this task is consistent with a configural model rather than with a moment-by-moment model. Moment-by-moment updating predicts that if speed is encoded incorrectly, the ratio of encoded length to actual length should be a constant; that is, the encoding function should have an intercept of 0. The fact that the encoding functions for length had a positive intercept and slope less than 1 (signifying that the short legs were encoded as too large and that the long legs were encoded as too small) is thus inconsistent with moment-by-moment updating. A similar argument can be made for the encoding of turn. Additional evidence against moment-by-moment updating was reported by Loomis et al. (1993), in the form of an increase in latency to initiate the return to origin, as outbound-path complexity increased.

We next turn to discussion of the issues addressed in the present research: (i) whether path integration is context-dependent and if so, how rapidly it adapts to recently experienced distances and turns; (ii) whether effects of experience can be specifically attributed to changes in the encoding process, and if so, what changes; and (iii) whether the encoding process represents distances and turns in a single path without considering its spatial relation to other paths (i.e., object-centered representation).

Relation of the encoding functions to experience with traveled paths

In its general form, the encoding-error model assumes only that all systematic error occurs during encoding. Based on the analysis of the Loomis et al. (1993) data, as just described, we consider a more specific version of the model, which assumes linear encoding functions. A third level of specificity for the model is one that adopts not only the linearity assumption, but also the parameters of the linear encoding functions that were estimated by Fujita et al. (1993). There are indications that these more specific versions of the model, at least, are limited in applicability: When extended to data from subjects who completed pathways more complex than a triangle (from Klatzky et al. 1990), fits of the linear model were considerably worse, and the parameter estimates differed from those derived from the Loomis et al. data. This may reflect the contribution of higher-order processes based on the configural properties of the stimuli, as are found in memory for maps (MacEachren 1992; Tversky 1981).

Even when constrained to the domain of relatively simple stimuli, the encoding-error model raises a number of issues. One concerns whether and how the encoding functions vary with experience. At the outset, we consider two mutually exclusive hypotheses about the influence of prior experience, in the context of the encoding-error model: (1) The encoding function is immutable, being independent of the past experience of a navigator, and (2) the encoding function depends upon the history of navigated pathways. If the function is immutable, then the parameter values fit to the Loomis et al. (1993) data by Fujita et al. (1993) are presumably the operative ones, and they should be found regardless of the nature of other pathways in the immediate context.

The assumption of immutable encoding seems, a priori, to be doubtful. Encoding of pathways on the scale of tens of meters is unlikely to use the same mapping as is used for pathways on the scale of under 10 m. In contrast to the immutability assumption, Maurer (1998) has recently proposed a model in which path integration is based on an estimate of distance that is assimilated to the average or maximal value in the animal's home range. Work

with humans indicating adaptation to many stimulus properties (Helson 1948) indicates that assimilation to navigational experience should occur, but the scope over which it occurs for human path integration is still an open question. Assuming that the encoding function varies with experience, one can ask whether the dependence takes into account only the most recent pathways, or is temporally more extended.

In order to manipulate experience, Experiment 1 varied the region of values of leg lengths and turns that a navigator experienced while traversing outbound legs of a number of paths. To see how this might affect the encoding process, consider that the leg-length encoding function estimated by Fujita et al. turned out to be highly accurate at the mean (equivalently, midpoint) of the stimulus values used in the Loomis et al. experiment, i.e., 4 m. If one assumes an encoding function that is constant regardless of context (which we doubt), then legs of 4 m would be encoded accurately regardless of the experienced leg lengths. If, in contrast, accuracy at the 4-m value reflects regression to the mean of values to which the navigator was exposed, then the encoding function should differ for sets of paths having a different mean from that of Fujita et al. Further, if adaptation to the local encoding context is rapid, then the encoding function should vary when the same navigator shifts from one region of leg lengths or turns to another within a short period of time. In Experiment 1, subjects experienced different regions of variation in leg length and turn over the course of a single session. The study asked not only whether the encoding function of Fujita et al. would be used, but whether these within-session variations would lead to differences in the underlying encoding functions and hence in the pattern of responses.

Another way in which the region of stimulus parameters could affect the estimated encoding function occurs if that function is globally nonlinear. Fujita et al. (1993) noted that although linear encoding functions were derived for the Loomis et al. (1993) data, the encoding function for turn was unlikely to be strictly linear over its entire range. Presumably, turns of zero and 180° would be encoded relatively accurately (Klatzky et al. 1990; Sadalla and Montello 1989). A finding of linear functions that differed in slope at differing regions might reflect a single underlying encoding function, but one that only locally approximated linearity.

Experiment 1 included a further manipulation that is likely to affect the encoding function; subjects navigated the path with no vision or partial vision. If the encoding function is not immutable, and if partial vision produces better discrimination among the distances and angles in the outbound paths, the encoding function should be steeper than in the no-vision condition.

Object-centered representation vs. relative spatial disposition

The encoding-error model implicitly assumes that the operative representation in path completion is what Marr (1982) called object-centered, where each path constitutes an object. The assumption is inherent in the model, because navigators are assumed to respond on the basis of encoded leg lengths and turns in a single path. The disposition of the paths relative to one another, or to a common external reference frame, is irrelevant under this model. It is reasonable to question whether navigators who complete a triangle on foot, without vision, have enough information about the local environment to anchor the path in an objective reference frame, as defined, for example, by the room or cardinal directions (cf. Rieser and Frymire 1995). Even without access to such referents, however, it is possible that subjects anchor the paths in a common space that is subjectively defined. For example, they might represent all the paths as having a common origin and direction of the first leg. This would allow them to relate the paths to one another, even if they did not know where they lay relative to an objective spatial frame. In this case, the subject would not be using an object-centered representation, and the spatial layout of the set of paths might affect performance.

Experiment 2 addressed whether subjects represent the disposition of the paths relative to one another by using a common reference direction, and more specifically, whether they compute the response in terms of that reference direction, or the return course. The course is the direction of a linear segment in space, relative to a reference direction (e.g., North). Course differs from turn in that a common reference direction is used for course values across all paths, whereas the response turn is the angle between the second outbound leg for a given path and the return leg. In the previous study of Loomis et al. (1993), subjects made only rightward turns on the outbound path. As a result, there was little variability in the course of the return leg: If the direction along the first leg is called North, the return course was predominantly to the Southwest. In the present study, we manipulated variability of return course across paths, while at the same time holding the distribution of response turns constant. The manipulation was intended to affect subjects' ability to determine the course response.

Classical paradigms in which subjects must discriminate between similar responses over trials produce substantial interference effects (see, e.g., Crowder 1976, Chapters 7–8). We hypothesized accordingly that low variability in return course would produce memory-based interference, essentially resulting in noise or uncertainty about the correct value of return course. Fujita et al. (1993) further proposed that the reduction in the range of responses observed by Loomis et al. (1993) was a result of such uncertainty; that is, lacking precise information about the correct response, subjects

moved all responses toward the mean. This reasoning was supported by Hayashi, Fujii, and Innui (1990), who found that the exponent of the power function for distance estimation decreased with memory load – essentially a reduction-of-range effect. Klatzky (1999) found that in the task of completing a triangle haptically, on a table top, the range of angular responses was severely reduced when subjects had to mentally rotate each path before responding. In summary, in Experiment 2, low variability in correct return course was proposed to cause interference and a consequent reduction in the range of the course responses relative to the correct course values, increasing error. This should occur, however, only if subjects represented the similarity in return courses, which requires relating the various pathways to a common reference direction. If, in contrast, subjects adopted an object-centered representation, as proposed by the encoding-error model, there is no reason for them to process the distribution of return courses and hence no reason to be subject to effects of its variability.

Experiment 2 also allowed encoding functions to be fit to the data from subjects having different experience with outbound paths. More specifically, it asked whether greater variation in a feature of the outbound-path – turn or leg length – would result in finer discriminations among values, producing a steeper encoding function for that feature.

Data analyses

The responses in the present studies are the turn and distance people walked when attempting to return to the origin of travel for a given path. The approach to data analysis is twofold: The first type of analysis works with the raw data. Where a variable is expected to influence overall error, analyses can be conducted on data pooled over the stimulus paths. We are generally more concerned, however, with functions relating the subjects' responses to the correct values for the individual paths (*response vs. correct* functions). For each condition of interest, there are distinct functions for response turn and response distance; in Experiment 2 a response course function is also considered. The response vs. correct functions are generally highly linear, so that each can be described by a slope and intercept parameter. Signed error is indicated in these functions by whether the response value is above or below the diagonal, which represents correct performance. The second type of analysis fits the encoding-error model to the average data, to extract a function describing subjects' encoding of turn and distance values in the outbound paths. Following Fujita et al. (1993), we assume a priori that this function is linear. Thus, fitting the model generates one linear function relating encoded turn to actual outbound turn and a second linear function relating encoded

distance to actual outbound distance; each of these functions has a slope and intercept parameter.

Experiment 1

Subjects completed a triangle after having been led through Leg-A, Turn-1, and Leg-B; in completing it they executed Turn-2 and Leg-C. The critical variables were (i) the "path feature" that was manipulated (Leg-A or Turn-1), and (ii) the "region" of possible values from which that feature was drawn (small or large values). These variables were combined in a series of distinct blocks of trials. When Leg-A was the manipulated path feature, subjects were exposed to a series of paths where the Leg-A lengths were all within either a region of small values (1–3 m) or a region of large values (4–6 m). In these conditions, Turn-1 varied relatively little. When Turn-1was the manipulated path feature, subjects were exposed to a set of Turn-1 angles that were all within either a region of small values (10°–70°) or a region of large values (110°–170°), and in these conditions, leg lengths varied relatively little.

In analyzing the empirical data and fitting the model, we considered the two general hypotheses described above. First, there might be no effect of experience with recent paths on the encoding of new parameter values. In this case, the encoding function found previously by Fujita et al. (1993) should apply to the current data, regardless of the region of the manipulated para- meter. Second, and more likely, the encoding function might be adapted to expectations or context. In this latter case, adaptation could be rapid enough to occur within each block of this experiment, or it could be more extended in time.

If the Fujita encoding functions are applied to the paths in Experiment 1, they predict a function relating responses to correct values that shows a general pattern of over-responding when response values are relatively low, and under-responding when they are high. This predicted function is shown in Figure 1 for each of the manipulated path features and measured responses. The functions tend to cross the diagonal at a point slightly rightward of the mean of response values, reflecting differences in the distribution of response values in this experiment as compared to that of Loomis et al. (1993).

If navigators rapidly adapted to variations in the present path features, they might form distinct encoding functions for each block of trials, each regressing to the mean of the region used in that block. In that case, the path having the mean values of Leg-A, Leg-B and Turn-1 (the "average path") within each region would be encoded correctly, and Leg-C and Turn-2 responses to that path would take on the correct values. Because of the experimental design, the function relating responses to correct values should then cross the diagonal near the mean of correct values. This would occur
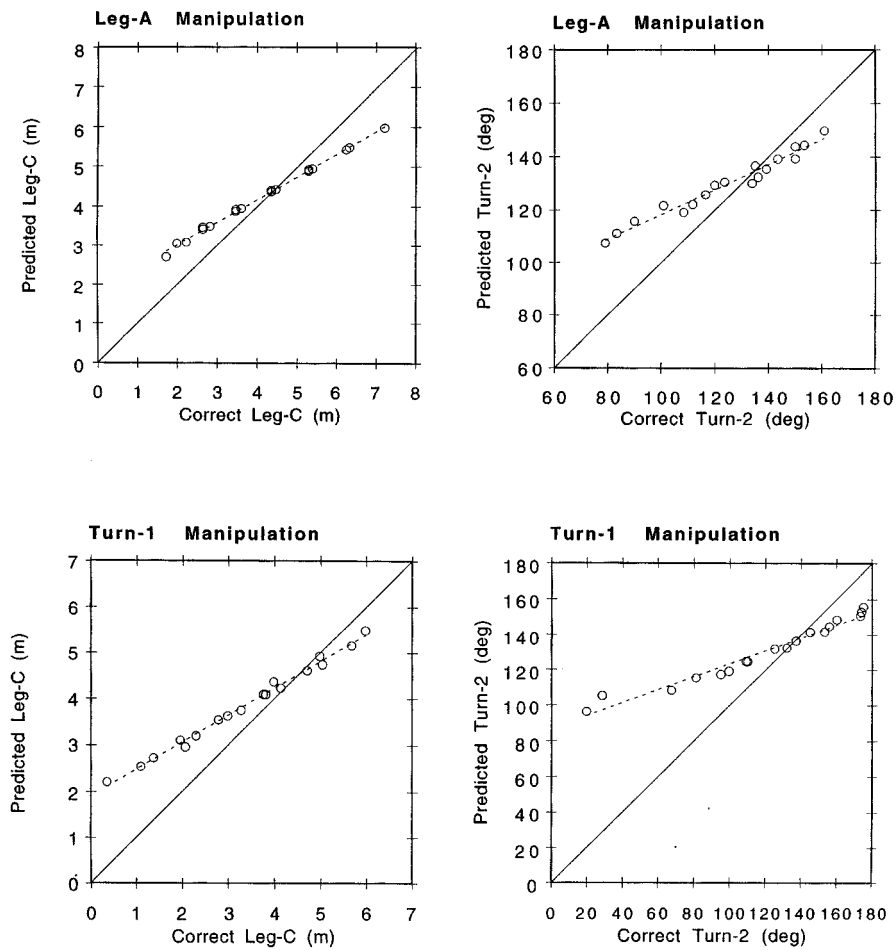
Figure 1. Predicted value of Leg-C and Turn-2 responses for the paths in Experiment 1, using the parameters of encoding functions derived by Fujita et al. (1993). The best-fit linear function is applied globally to the entire parameter range.

within each region, and for each response. As a result, the manipulation of region should produce two distinct functions relating responses to correct values, with the means of response values tending to match the means for the low and high region of correct stimulus values separately. Predicted responses generated from the Fujita et al. encoding functions, but applied to each region separately, are shown in Figure 2. For these purposes, the slopes of the Fujita encoding functions were imposed, but the intercepts were adjusted to produce regression to the mean values of the present path features, so that the within-region mean of a given path feature would be encoded accurately. The
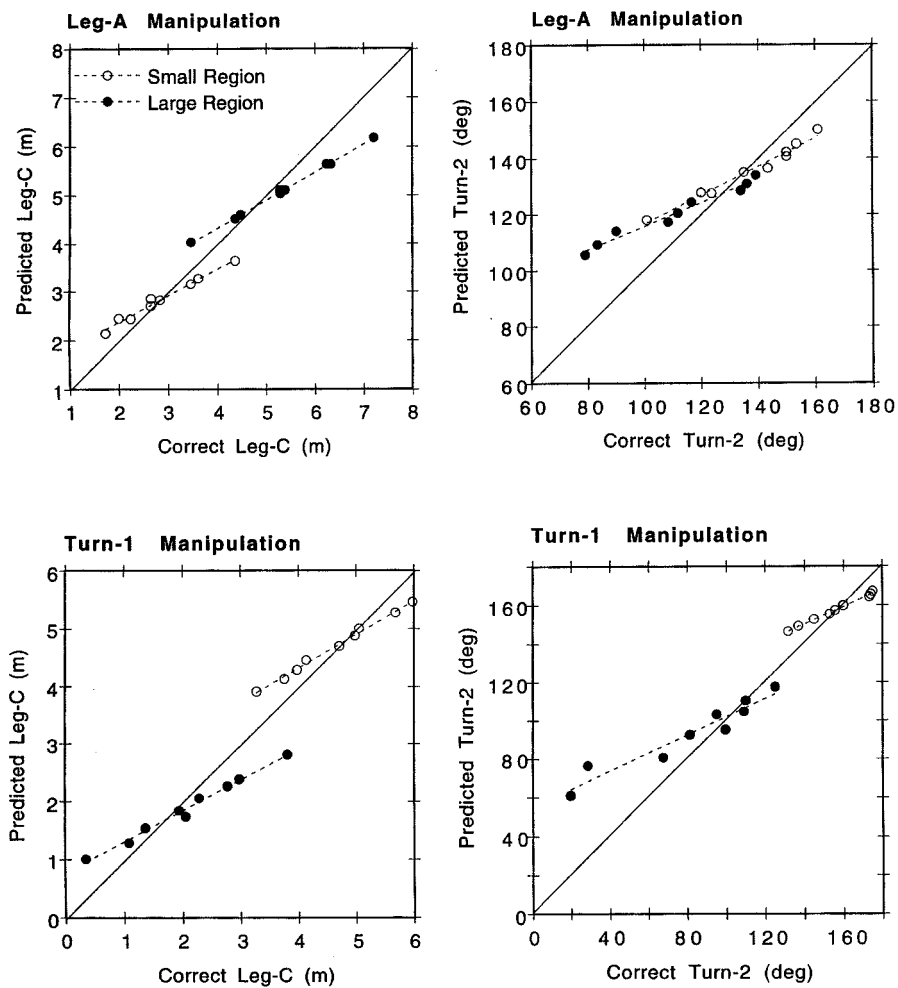
Figure 2. Predicted value of Leg-C and Turn-2 responses for the paths in Experiment 1, generated by applying the model of Fujita et al. (1993) locally to each parameter region. The slopes of the encoding functions derived by Fujita et al. were combined with intercepts that would force accurate encoding of the mean of the values within each region. Best-fitting linear functions are shown for each region.

adjusted encoding functions were then used to generate the predicted turn and distance response shown in the figure.

A third alternative is slow adaptation to experience. Consider that subjects bring generalized expectancies such as anticipated room size to the task. They may also adapt slowly across the entire session rather than being block by block. In this case, discrete functions relating responses to correct values within each region would not be seen (cf. Figure 2). If subjects happened to

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arrive at an encoding function that regressed to the overall mean of stimulus values, as in the case of Loomis et al. (1993), then there would be a single empirical function relating responses to correct values that crossed the diagonal near the mean of correct values, pooled across regions. However, just because the function fails to show distinct regions does not mean that it must cross the diagonal at the overall mean of correct values. Indeed, because trials were blocked by regions of feature values, subjects would not be exposed to the entire distribution of values until relatively late in the study, which would work against assimilation to the mean experimental value of leg length or turn.

An additional manipulation was whether subjects had occluded vision (with diffuse light only) or whether they could see 1.5 m ahead along the path, allowing optic flow from the floor and sight of the turn angle as the two outbound legs intersected. This manipulation was intended to provide a broader test of the encoding-error model. If regression to the mean in encoding stimulus values reflects poor sensory information, and if vision improves encoding, then the function relating response values to correct values, as well as the estimated encoding functions, should have a slope closer to 1.0 and an intercept closer to 0.0 in the condition with partial vision.

Method
Subjects. The subjects were 7 male and 7 female university students paid to participate; genders were split across groups as equally as possible.

Stimuli. The subject's task on each trial was to complete a triangle after having been led on a leg of varying length (Leg-A), through a rightward turn of varying size (Turn-1), and then along a second leg that was always 2 m in length (Leg-B). The subject then made a second turn (Turn-2) and walked a third leg (Leg-C), in order to respond. Each subject took part in trials with 36 distinct triangular paths, with each path replicated twice, for a total of 72 trials. The paths were divided into four sets, defined by the manipulated path feature (Leg-A length or Turn-1 angle), and the region of values of that feature (small or large). In the small-leg set, Leg-A was 1, 2, or 3 m, and in the large-leg set it was 4, 5, or 6 m; each of these values of Leg-A was combined with 3 Turn-1 values – 60°, 90°, or 120° – to create 9 triangles per set. In the small-turn set, Turn-1 was 10°, 40° or 70°; in the large-turn set it was 110°, 140°, or 170°; each of these values of Turn-1 was combined with Leg-A values of 2, 3, and 4 m, to create 9 triangles per set. Presentation of the sets was blocked, as described below.

Apparatus. The experiment was conducted within an experimental space 7.9 m × 8.0 m. The first leg of each path was marked in tape; the second leg

was a 1.74-m metal strip that was put into place at the correct angle at the start of each trial, so that in stepping just beyond it, the subject completed the 2-m length desired for the second leg. The subject was guided on the first two legs of the triangle by holding onto a bar held by the experimenter, then attempted to return to the origin. A Sonin 250 transmitter and two receivers were used to determine the endpoint of travel by trilateration. No feedback was given. The subject was led circuitously to the origin between trials; subjects generally report that they are unable to track the origin's location under these conditions.

In the vision condition, the subject could see only 1.5 m in front. A bicycle helmet was altered by adding an opaque visor that limited side vision (Sadalla and Montello 1989), and the visor tilt was adjusted for each viewer to limit sagittal head movement and enforce the viewing distance. To implement the no-vision condition, subjects wore not only the helmet but also eye covers that allowed light but not pattern vision. An omnidirectional microphone and earphones were also used, so that sound was sent to the ears from a fixed location in the room, regardless of point of origin (see Loomis et al. 1993; Rieser et al. 1986).

Design and procedure. The presence/absence of vision was manipulated between subjects; the path feature and region manipulations occurred within subjects in four distinct blocks of trials. In each block a set of 9 paths, corresponding to a single manipulated path feature and region, was presented, with each path in the set repeated twice. A Latin Square was used to order the blocks across subjects. The two replications of a set of paths within a block occurred in succession (i.e., all 9 paths were presented before any was repeated); the path order was otherwise random. At the end of the block, there was a break while the experimenters prepared the next paths and the helmet was recalibrated for subjects in the vision condition. Subjects were outside the room when the helmet and earphones were installed and during recalibration.

Results

The stopping location was used to compute two response measures, a turn angle toward the origin at the end of Leg-B (i.e., Turn-2) and a walked distance (i.e., Leg-C). The computation assumed that subjects turned in the direction that yielded a turn angle of less than 180° and did not veer. Due to experimenter error, 4 trials had missing scores, and the value from the other replication trial was substituted for the missing value.

Replication effects. Data were initially examined for replication effects, which compared (within each condition) the two replications with respect

to the slopes and intercepts of functions relating responses to correct values (the response vs. correct functions). As these 32 tests had only 2 significant outcomes (one is expected by chance), the two replications were combined for further analysis. Note that this does not simply reflect low statistical power; the data were very similar across replications.

Average signed error. Table 1 reports the mean of correct and response values across paths, subjects, and replication for each condition (defined by manipulated path feature, region, and visual status) and each response measure (Turn-2 and Leg-C). To determine effects of region and visual status, separate analyses of variance were conducted within each manipulated path feature and response measure. Vision reduced error; the effect was at least marginally significant in three out of the four cases tested: the Leg-C measure when Leg-A was manipulated, $F(1,12) = 11.06$, $p < 0.01$; the Turn-2 measure when Leg-A was manipulated, $F(1,12) = 5.18$, $p < 0.04$, and the Leg-C measure when Turn-1 was manipulated, $F(1,12) = 3.90$, $p = 0.072$. The effect of region was also significant in all four ANOVAs: the Leg-C measure when Turn-1 was manipulated, $F(1,12) = 9.00$, $p < 0.025$, the Turn-2 measure when Turn-1 was manipulated, $F(1,12) = 11.80$, $p < 0.01$, the Leg-C measure when Leg-A was manipulated, $F(1,12) = 33.42$, $p < 0.001$, and the Turn-2 measure when Leg-A was manipulated, $F(1,12) = 4 72$, $p = 0.05$. These region effects simply reflect the overall tilting of the data away from the diagonal. Although the tilt appears to be more symmetric about the mean when vision is present, in no case did visual status interact with region.

Response vs. correct functions. Figure 3 shows the average response vs. correct functions for each response measure (Leg-C and Turn-2), within each of the four conditions defined by visual status and manipulated path feature. Subjects tended to over-respond when correct values were relatively small and under-respond when correct values were relatively large, as was found by Loomis et al. (1993). Linear functions provided a good fit to each response and condition, as shown in the figure.

Although the combined-region functions shown in Figure 3 fit the data well, it is also possible to fit two functions to each condition, one for each level of region from which stimulus values were drawn (large vs small). We used t-tests to compare parameters (slope, intercept) of separate functions defined by region. This amounts to fitting separate functions to the data represented by squares and circles in Figure 3 and comparing the regression parameters. Of the 8 comparisons, there were significant parametric differences in 5 cases. These cases all indicated a flattening

Table 1. Experiment 1: Mean of correct values for each response – Leg-C (m) and Turn-2 (deg) – and mean of responses, by visual status, manipulated path feature(Turn-1; Leg-A) and region of that feature (small values, large values, and pooled over region)

| Manip. parameter and response	Small values			Large values			Pooled over region		
	Mean of correct values	Mean response, vision	Mean response, no-vision	Mean of correct values	Mean response, vision	Mean response, no-vision	Mean of correct values	Mean response, vision	Mean response no-vision
Turn-1									
Leg-C	4.62	4.28	3.89	2.08	2.31	2.06	3.33	3.30	2.98
Turn-2	156.12	152.17	161.06	81.73	86.94	104.83	118.92	119.56	132.94
Leg-A									
Leg-C	2.84	3.01	2.68	5.34	4.76	4.06	4.09	3.88	3.37
Turn-2	137.47	131.33	149.56	110.93	110.89	125.06	124.20	121.11	137.31
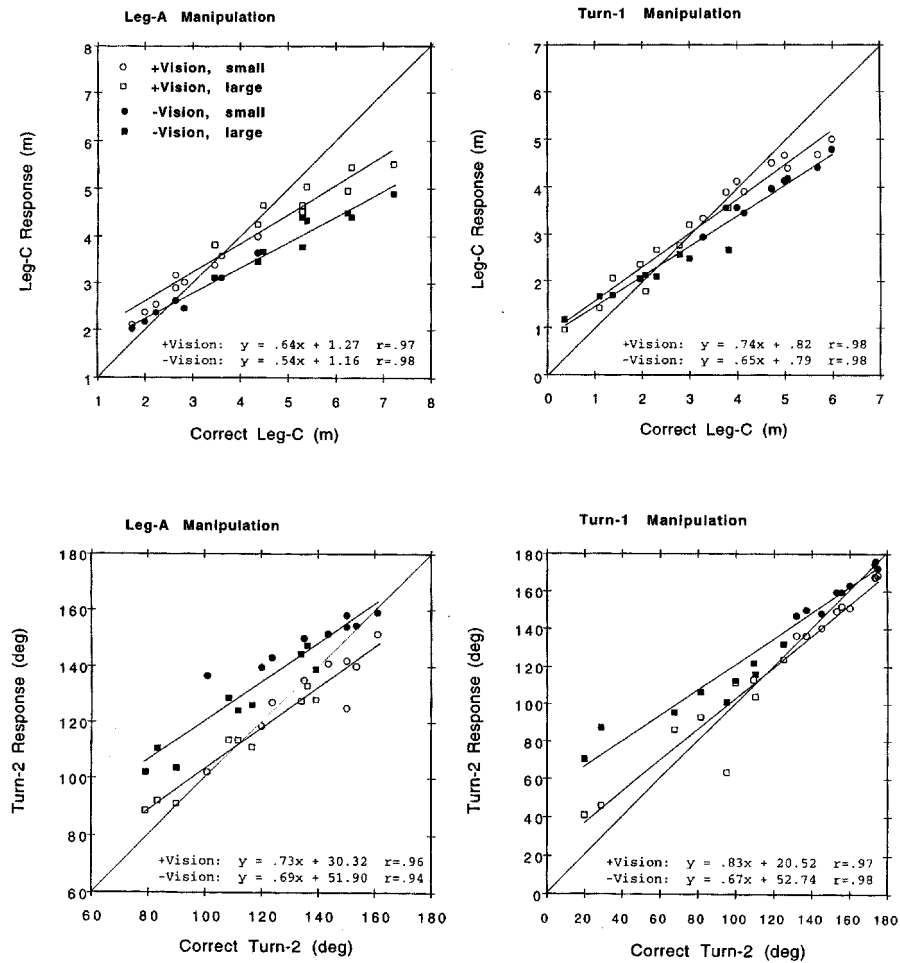
Figure 3. Experiment 1: Correspondence between response value and correct value for each manipulated path feature (Turn-1, Leg-A), each response measure (Turn-2, Leg-C), level of visual status (vision, no-vision) and region of path feature (small, large). Linear functions are fit separately by visual status but not by region.

of the response-vs-correct function at its upper end, resulting in a higher intercept and lower slope for the function fit to the responses closer to that end. In essence, these comparisons capture a subtle but fairly regular nonlinearity of a typical psychometric form. As this nonlinearity accounts for little variance (on average, 6%), and it does not follow the predictions based on regression of encoding parameters to the mean of experienced values within a region (see Figure 2), it will not be discussed further. Note too that simulations showed that the same nonlinearity can be generated by a

Table 2. Experiment 1: Parameter values from encoding-error model fit separately by manipulated path feature (Turn-1, Leg-A) and visual status

	Length slope	Length intercept (m)	Angle slope	Angle intercept (deg)
Turn-1 manipulated, vision	0.66	0.77	0.84	14.61
Turn-1 manipulated, no-vision	0.60	0.55	0.86	0.08
Leg-A manipulated, vision	0.73	0.72	0.72	30.09
Leg-A manipulated, no-vision	0.52	0.66	0.82	0.81

single encoding function applied across regions; it does not by itself indicate separate encoding functions at the two levels of region.

Fitting the encoding-error model. The encoding-error model was fit to the data by assuming that subjects (a) encoded the lengths of Legs A and B by a linear function that mapped stimulus values to internalized values, (b) also encoded the angle of Turn-1 by a linear function, (c) computed the return trajectory from the encoded values without systematic error, and (d) executed the return trajectory without systematic error. The model was fit separately for each combination of manipulated path feature (Turn-1, Leg-A) and visual status. Initially, versions were evaluated that fit the data over both regions of the path feature simultaneously and to each region separately (the latter doubled the number of parameters). Because there was no advantage in goodness-of-fit for the two-region model, we will focus on the model that assumes common encoding functions across both regions of the manipulated path feature. This model has 4 parameters: the slope and intercept of the encoding function for leg length, and the slope and intercept of the encoding function for turn. Best-fitting parameters were found by using a routine that minimized the Euclidean distance between the subject's empirically determined response endpoint and the model-predicted endpoint, summed over all paths in the condition under consideration. Table 2 shows the parameters of the encoding function for each of the four conditions. As was the case in Fujita et al. (1993), the functions showed slopes considerably less than 1.0. However, substantial positive intercepts were not always evident.

To evaluate the model, we considered 8 sets of model-predicted data, corresponding to 4 conditions (defined by manipulated path feature and visual status) and 2 measured responses (Leg-C and Turn-2). The correlations between predicted and observed responses averaged 0.97, and the slopes relating predictions to observations also averaged 0.97, across the predictions.

As was explained in Fujita et al. (1993), however, it is relatively undemanding for a model to make ordinally correct predictions that will be positively correlated with the observed *responses*. A more demanding criterion for goodness of fit is to predict *signed errors* in the responses. Considering this test, the model produced correlations between predicted and observed signed error averaging 0.86, and the slope of the function relating predicted error to actual error averaged 0.84. These predictions of signed error are somewhat worse than those obtained previously for the Loomis et al. (1993) data by Fujita et al., where the correlation between predicted and obtained signed error averaged 0.92 and the slope averaged 1.08. However, the Loomis data were based on a larger N.

The data generated by the model showed the obtained effect of visual status; that is, the mean of predicted Leg-C was greater for the vision condition and the mean of predicted Turn-2 was greater without vision, as was observed. The model did not, however, predict the small nonlinearities that led to the effects of region in the data (nor did models that were fit separately by region).

Comparison to Fujita et al. model. Comparison of the parameters of the present no-vision functions with those estimated by Fujita et al. (1993) for other no-vision data (from Loomis et al. 1993) indicates that the values are quite different. Averaging over the two manipulated path features (Leg-A and Turn-1), the slope for the leg-length encoding function was 0.56 and the intercept was 0.60 m (cf. 0.60 and 1.2 m for Fujita et al.). The slope and intercept of the presently derived turn-encoding function averaged 0.84 and 0.4° (cf. 0.48 and 44° in Fujita et al.). The differences in the functions estimated by Fujita and for the present data contraindicate the use of a highly general encoding function. We further evaluated the generality of the encoding functions by using the Fujita parameters to predict the present data. The correlations between responses predicted by the Fujita parameters and observed responses for Leg-C and Turn-2 were all high (0.94 or better); however, there were systematic errors in the predictions. This can be seen in Figure 4 (upper panels), which shows the relation between the observed responses and the Fujita predictions (generated as for Figure 1), for two of the four combinations of path feature and response (the others showed similar goodness of fit). Shown for comparison (lower panels) are the observed responses against the present model's predictions for the same conditions (again, the others were similar in goodness of fit). On balance, we conclude that the Fujita et al. functions were not used to encode the present stimuli.

In further departure from the Fujita et al. model, the presently obtained encoding functions did not produce a general pattern of regression to the
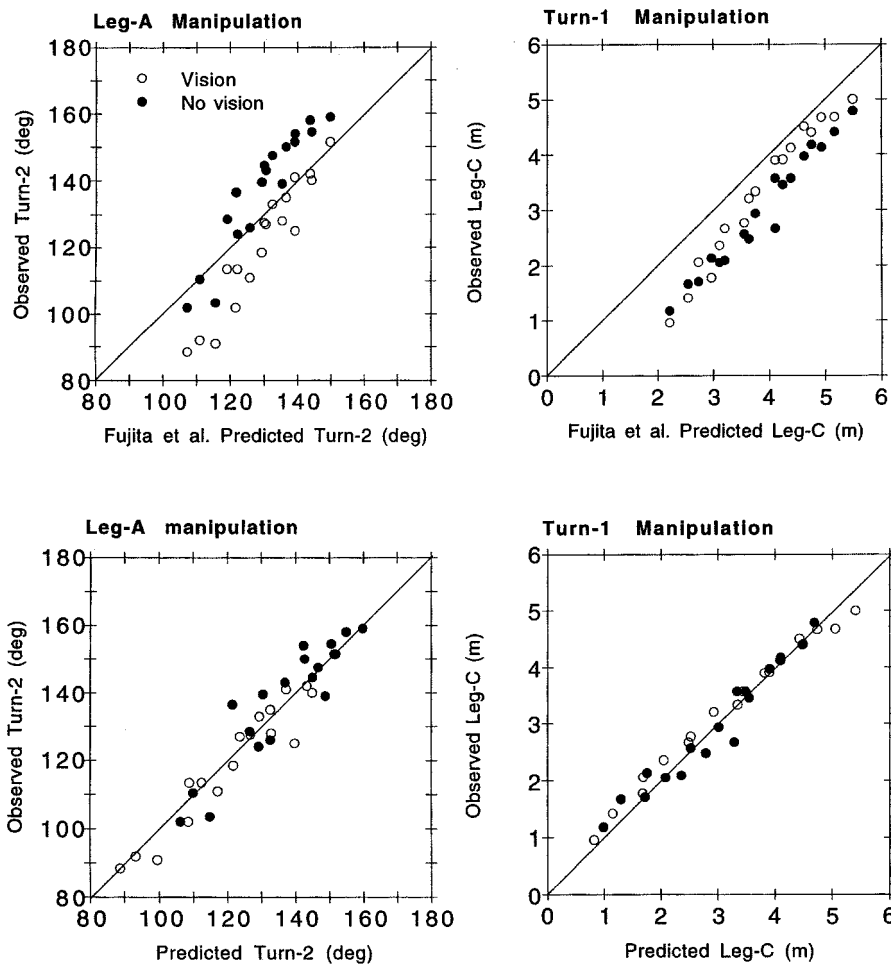
Figure 4. Upper panels: Relation of observed responses, with and without vision, to predictions for Experiment 1 from the Fujita et al. (1993) parameters, for two of the four combinations of manipulated parameter (Turn-1, Leg-A) and response (Leg-C, Turn-2). Lower panels: Relation of observed responses to predictions from the model fit to the data, for the same conditions.

mean of encoded values, which would lead to encoding the mean stimulus value correctly. Values that would be encoded without error, given the mean parameters estimated in the no-vision conditions, would be a leg length of 2.8 m and a turn of 123°, as compared to the mean stimulus values of 2.6 m and 90°. It should be noted too that the no-vision data did not show greatest response accuracy near the mean of correct values.

Discussion

Overall, the data indicate that encoding is experience dependent, but not on a block by block basis. Consider first the results when vision was fully occluded. The data showed a similar pattern to Loomis et al. (1993), in that subjects compressed the range of responses, and as a result, linear functions fit to the data relating responses to correct values had slopes less than 1.0. The results did not, however, show matching of the mean of responses to the mean of correct values, instead showing an overall pattern of overturning and underwalking. The failure of subjects to assimilate encoding to the overall mean may reflect the blocking of feature values, which meant that the full range would be known only relatively late in the experiment.

These data did not show that responses were assimilated to experienced values separately at each region of the manipulated stimulus features. Substantial variance was accounted for by a single function fit across regions of the manipulated feature; there were not two obviously discrete response vs. correct functions that crossed at regional means. Moreover, there was no evidence of a change in performance between the two replications of a particular region of stimulus values, as might be expected if subjects used the first replication to learn about the values and adjust the encoding function.

Partial vision reduced error, so that responses were closer to the diagonal of the response vs. correct function. The mean Leg-C response was within 0.2 m of the mean of correct values, and the mean Turn-2 response was within 3° of the mean of correct values. The degree to which the range of responses was compressed, relative to correct values, did not decrease when partial vision was supplied, although overall accuracy increased. This is not what was expected. That is, whereas one might have expected vision to increase sensitivity to variations in the stimulus, and thereby to increase the slope of the function relating responses to correct values, the increase in accuracy due to vision was reflected in the intercept of the function. Moreover, the parameters of the encoding functions fit to the data did not show a systematic increase in slope with vision.

An encoding-error model that fits linear encoding functions to the data accounted for a substantial amount of variability in signed error and produced the observed effects of visual status. The parameters of the model were quite different from those found by Fujita et al. (1993) for the Loomis et al. (1993) data. Moreover, when the Fujita parameters were used to predict the present data, the model-predicted responses showed systematic deviations from the observed responses. Thus it appears that the Fujita et al. parameters are not broadly generalizable. Another indication of this can be seen in Table 2, which shows that the parameters fit to the data differed even between the

two sets of paths used in the present experiment, one set manipulating Turn-1 and the other manipulating Leg-A.

Experiment 2

The task in Experiment 2 was again triangle completion. Its primary purpose was to investigate whether variability in return course affects performance in triangle completion. Recall that the return course is the angle between the return leg and a reference direction, which we arbitrarily aligned with the direction of outbound travel along Leg-A. Two groups of subjects took part, one having high variability in return course and another low variability. While the course varied, the response turn values were identical for the two groups.

As was explained in the introduction, the encoding-error model's assumption of object-centered representation would not predict an effect of variability in return course, because the variability can only be known if the spatial disposition of the different paths is represented relative to a common reference direction. In that case, low variability in return course is hypothesized to produce memory-based interference, leading to a reduction in the range of the course responses relative to the correct course values and hence increasing error.

The second purpose of the study was, as in Experiment 1, to determine whether different encoding functions would result from different experience with oubound path features. A specific hypothesis is that greater variability in a parameter of the outbound path sensitizes navigators to that parameter, so that they differentiate the parameter values to a greater extent. This would result in a steeper encoding function for more variable parameters. The outbound path features are shown in Table 3 and will be discussed in more detail in the Method section.

Method
Subjects. Subjects were 16 individuals (8 males, 8 females) from the university community who were paid for a single 2-hour session. They were assigned to two groups with 4 males and 4 females in each.

Stimuli. Subjects were blindfolded and exposed to 32 trials, comprising 3 replications of 8 different experimental paths and an additional set of 8 filler paths. The experimental configurations are those shown in Figure 5, and their parameters are shown in Table 3. Unlike Experiment 1, Turn-1 could be either rightward or leftward. The triangular configurations that were experienced by the two groups were actually identical. What differed was the direction in which the legs were traversed, and hence which legs and turn were outbound and which were produced as the response. Note that the magnitude of the

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Path #	Drop-off point re ref. direction	Leg-B (m)	Turn-1 (deg)[a]	Leg-C (m)	Turn-2 (deg)[a]	Return course (deg)
Variable return						
1	15	6.20	−175	2.25	−170	195
2	60	5.48	−159	2.25	−141	240
3	105	4.05	−148	2.25	−107	285
4	150	2.34	−151	2.25	−59	330
5	195	1.92	162	2.25	33	15
6	240	3.47	146	2.25	94	60
7	285	5.07	155	2.25	130	105
8	330	6.05	169	2.25	161	150
Variable outbound						
1	15	2.25	15	6.20	170	185
2	60	2.25	60	5.48	141	200
3	105	2.25	105	4.05	107	212
4	150	2.25	150	2.34	59	209
5	195	2.25	−165	1.92	−33	162
6	240	2.25	−120	3.47	−94	146
7	285	2.25	−75	5.07	−130	155
8	330	2.25	−30	6.05	−161	169

[a] Clockwise turn values are signed positively, counterclockwise negatively.

response turn (Turn-2) required of subjects was identical for the two groups, but was to be made in opposite directions.

The critical experimental manipulations were performed by using a circular arrangement for the various paths (see Figure 5). The drop-off points (the ends of Leg-B, from which the subject responded) were distributed around the circumference of a circle 4.5 m in diameter. The radii from the center of the circle to the drop-off points were walked by both groups, but at different points in travel, as follows. The variable-return group began each trial in the center of the circle, walked outside of it along a Leg-A of 4 m, turned, and moved along a Leg B to a drop-off point on the circumference of the circle, from which they were to return to the center along a radius. For these subjects, then, the radii of the circle constituted the Leg-C segments, and the broad angular distribution of these radii over the set of paths meant that this group had a variable return course. Conversely, the variable-outbound group originated each trial outside the circle, walked along a 4-m Leg-A into the center, and then turned and continued along a radius of the circle to a drop-
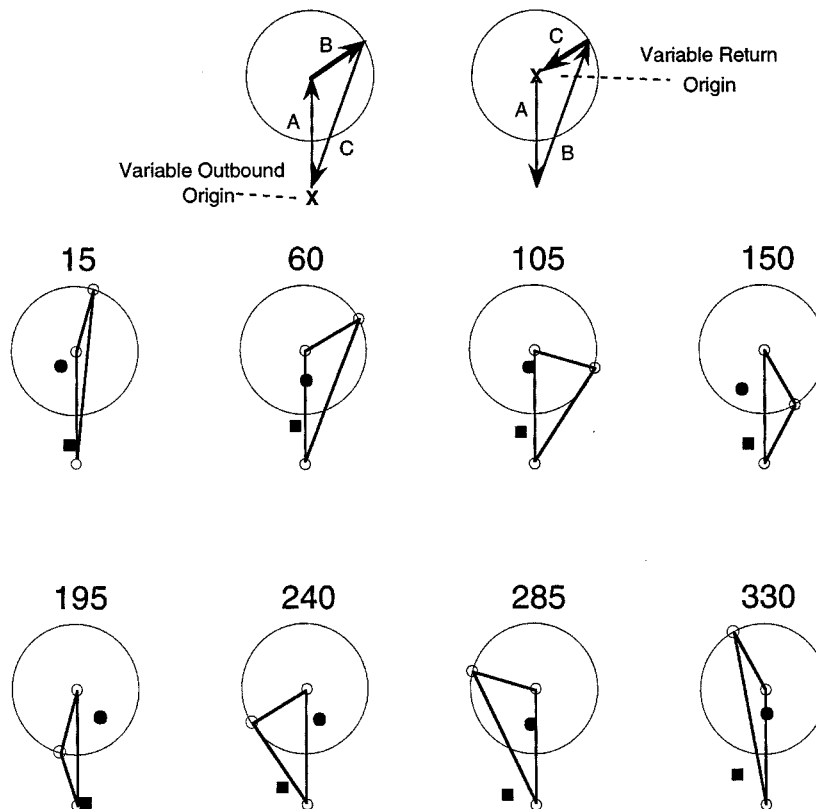
Figure 5. Row 1: Typical paths in Experiment 2 for each group, with X marking the origin and arrows indicating direction of travel along Legs A, B, and C. Row 2 and 3: The eight experimental paths relative to the circle on which dropoff points lay. Also shown is the centroid of responses for each path and condition (variable-return shown by dark oval, variable-outbound by dark square).

off point on the circumference. This group was called variable outbound, because it was the Leg-B segments that fell along the broadly distributed radii of the circle.

As a result of the path layouts, the two groups experienced differences in the variability not only with respect to course, but also in outbound path features. The group with variable outbound course also experienced (a) variable outbound turn (which was made in the center of the circle to face a point on the circumference) and (b) invariant outbound leg lengths on the experimental paths (Leg-A was constant at 4 m and Leg-B fell along a 4.5-m radius of the circle). Thus the group with variable return course experienced less variability in outbound turn and more in outbound leg-length (see Table 3).

Each experimental configuration was presented 3 times for each group. In addition, there were 8 filler paths presented once each, in which Leg-A length was either 3 m or 5 m instead of the 4-m length in the experimental trials. The order of path presentation was randomized, within the constraint that all 8 experimental paths were tested before any one was repeated.

Apparatus and procedure. The experiment was conducted in the same laboratory as Experiment 1. To minimize potential auditory distance cues, direct sound was attenuated by approximately 20 dB with hearing protectors, under which were small earphones. As in Experiment 1, the microphone signal was amplified and delivered to both ears, precluding localization but allowing verbal instructions to be audible.

The experimenter guided the blindfolded subject along the paths by maneuvering a horizontal bar that the subject grasped with both hands; the subject then attempted to walk freely back to the starting location. The observer's horizontal position in the workspace was sensed by a video tracking system described elsewhere (Klatzky et al. 1990), which sampled the observer's position at 30 Hz to an absolute accuracy of about 5 cm. Between trials the experimenter guided the subject back to the starting location via a circuitous path to avoid error feedback. On about 4% of the trials, a subject's response course erred enough to result in a possible collision with one of the laboratory's walls, in which case the trial was aborted and the data were eliminated.

Results

Only data from the 24 experimental trials (not the 8 fillers) were considered. From the position record of the walked homeward trajectory, measures of Turn-2 and Leg-C were derived. The response course was based not on the recorded trajectory (which could include veer), but on the angle between the dropoff point and the subject's stopping point for a given path (averaged over replications). The centroid of responses averaged over subjects, for each of the paths and groups, can be seen in Figure 5. Also shown is the correct response location. Figure 6 shows the mean response centroid and standard error.

Response vs. correct functions. Response measures include signed error in distance (Leg-C), turn (Turn-2), and course. Course was computed clockwise relative to the direction in which Leg A was traversed. Signed course error is the difference between the correct course and response course, signed according to the shorter direction from correct to response course. A positive sign means that the subject started along a course that was clockwise of the
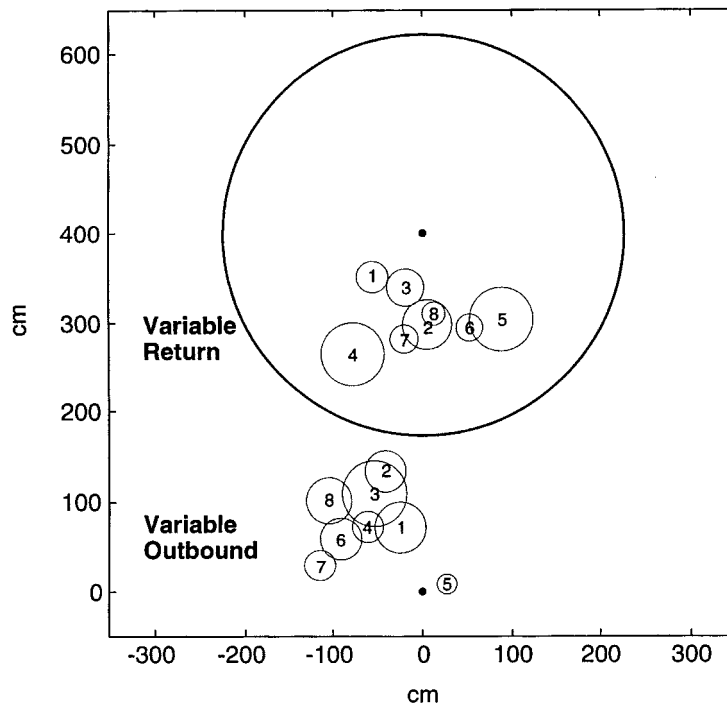
Figure 6. Experiment 2: Centroid of responses and standard error of the mean distance from centroid for the variable-return condition (upper cluster of points) and the variable-outbound condition (lower cluster). The circle is centered on the centroid of responses, the number in the center identifies the path (see Table 3), and the radius is the standard error. The correct endpoint is at the top of Leg A (vertical line in each path) for the variable-return condition and the bottom for the variable-outbound condition.

correct course (i.e., the response course would be reached sooner by going in a clockwise direction from the correct course than by going in a counter-clockwise direction). A negative sign means that the shorter direction from correct to response course is counterclockwise. Signed turn (Turn-2) error was computed as response turn minus correct turn, so that overshoots are signed positively and undershoots negatively. It was assumed that subjects always made the lesser of the two possible turns toward the origin, and no obvious violation of this was noted by the experimenter. Signed distance (Leg-C) error was also computed as response minus correct, with positive values indicating overshoots and negatives indicating undershoots.

Figure 7 shows the mean response course as a function of the correct course. A function fit to the overall data had a slope of 1.12 and a y-intercept of $-14.35°$, with an r^2 of 0.96. The lesser variability of return course in the variable-outbound condition did not produce a flatter region in the function,
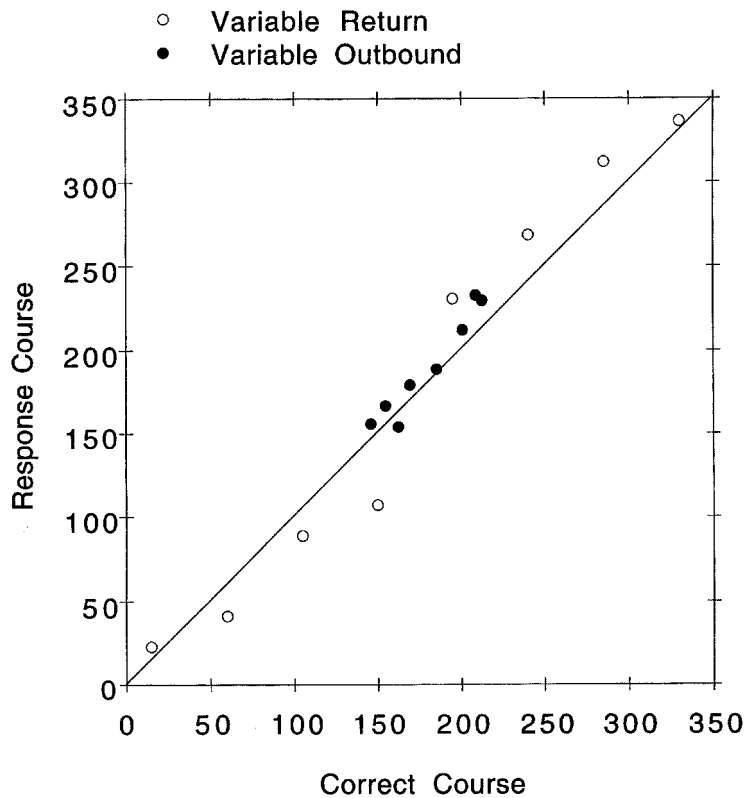
Figure 7. Experiment 2: Functions relating response course to correct course, by group (variable-return, variable-outbound).

corresponding to a reduction in the range of the course responses relative to the correct course values. Such a difference in slope between groups should produce a difference in absolute error even if both functions were centered on the diagonal (in which case mean signed error would not differ), but neither signed nor absolute error differed between groups, $p > 0.25$ for both measures.

Figure 8 (upper right panel) shows the response vs. correct function for Turn-2. Although the correct turn angles were identical for the two groups, the pattern of errors differed. Note in particular a stairstep pattern in the function relating the response turn to the correct turn within the variable-outbound condition. Because successive points on the x axis correspond to response turns of different direction (alternating first counterclockwise, then clockwise), this suggests a systematic effect of the direction of the response turn. (The course errors in Figure 7 had the same magnitude as turn errors but did not show the stairstep effect because they are signed differently.)
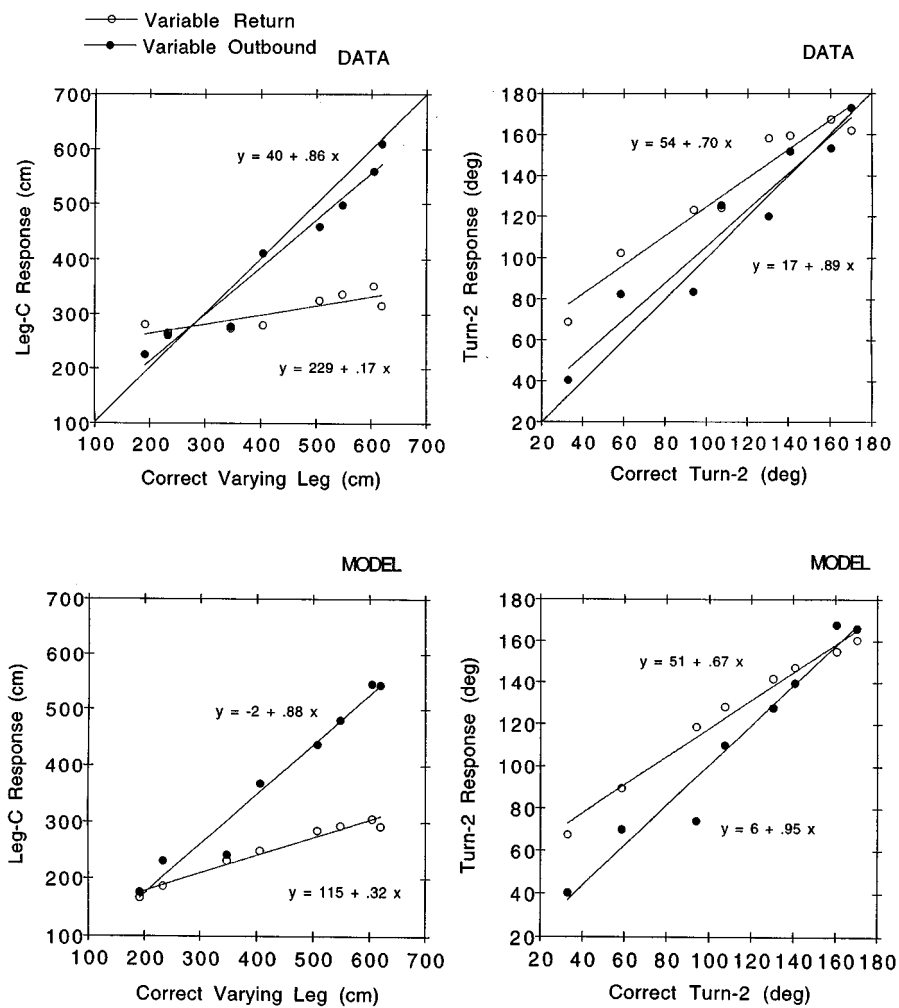
Figure 8. Experiment 2: Response value as a function of correct value for each response measure (Turn-2, Leg-C), by group (variable-return, variable-outbound). In the variable-return group, the varying leg is Leg-B, and in the variable-outbound group, it is Leg-C. Best-fitting linear functions are shown. The upper panels show data from the experiment; the lower panels show the predictions of the encoding-error model.

Figure 8 (upper left panel) shows Leg-C responses against the correct value of the varying leg in the path. In the case of the variable-outbound condition, the varying leg is the correct response leg, and we have the typical response vs. correct function. But in the variable-return condition, the correct response distance is constant, and the Leg-C response is accordingly plotted against the value of Leg B (the varying leg) in the corresponding path.

The data indicate that variable-return subjects, rather than responding with a constant Leg-C value, systematically varied their responses in accordance with the value of Leg B.

ANOVAs were conducted on signed error in Turn-2 and Leg-C, with factors of group (variable-return vs. variable-outbound) and path (8 values). The signed Turn-2 error ANOVA produced an interaction between group and path, $F(7,98) = 7.71$, $p < 0.001$. In the ANOVA on signed Leg-C error, the group X path interaction was marginal, $F(7,98) = 2.08$, $p = 0.05$. None of the group main effects on error was significant, indicating that the magnitude of error did not differ overall between groups, whereas the pattern of error did.

Evaluating the encoding-error model. We again used the encoding-error model to fit the data, with the same assumptions as before – linear encoding functions for leg length and turn, and accurate computation and execution of the homeward trajectory.[2]

The initial fit was poor. In contrast to the patterns evident in Figure 6, the model predicted that the variable-return group's responses for the various paths would be distributed around the origin, and the variable-outbound responses would fall about equally on each side of Leg-A, although they could fall above or below the origin. To understand why this is so, consider the predicted data if the subject's encoding is entirely attributable to mis-scaling the path (i.e., if Turn-1 angles are encoded perfectly and encoded leg lengths are a constant proportion of correct values; that is, the encoding function for leg lengths has a zero intercept). In this case, the shape of the subject's distribution of responses will mimic the distribution of dropoff points across the pathways, but will be off by a scale factor. In the variable-return condition, the actual dropoff points form a circle around the origin. If subjects under-encoded the distances, they will think they are in a smaller triangle, so they will go part way to the origin and stop, with the responses falling around a circle. If they over-encoded, they will pass through the origin, go a constant amount, and stop, with the response distribution still forming a circle. Similarly, in the case of the variable-outbound condition, the dropoff points form a circle far from the origin. With under-encoding, subjects will go toward the origin part way, and the responses will come together into a tighter circle. With over-encoding, they will go past the origin and spread apart, the response distribution still forming a circle. Although this is the expectation if encoding errors are entirely errors of scale, simulations indicated that these same patterns in the data would remain robust under a broad range of encoding functions for turns and leg lengths.

Given the systematic patterns in the data that were summarized above, a modified model was constructed. This model had 7 parameters and allowed

Table 4. Experiment 2: Values of parameters fit to the Variable-return and Variable-outbound data by the encoding-error model

Condition	Leg-A value (m)	Leg-B slope	Leg-B intercept (m)	Turn slope, path 1-4	Turn intercept (deg), path 1-4	Turn slope, path 5-8	Turn intercept (deg), path 5-8
Variable return	2.76	0.86	0.00	0.90	1.6	0.83	11.6
Variable outbound	3.53	0.89	0.00	0.89	8.6	1.33	−20.7

Note: In the variable-outbound condition, Turns 1-4 are clockwise turns and Turns 5-8 are counterclockwise; the reverse holds for the variable-return condition.

for (a) distinct linear encoding functions for left and right turns and (b) different encoding for Leg-A (encoded as a constant value) and Leg-B (encoded by a linear function). Based on the data, we anticipated that the model-derived encoding functions for left and right turns would be similar when the model was fit to the variable-return group, but would differ when the model was fit to the variable-outbound group (reflecting their different responses for left and right turns). We also anticipated that the estimate of the encoded value of Leg-A would be predictable from the encoding function for Leg-B when the model was fit to the variable-outbound group, but not when it was fit to the variable-return group (reflecting their dependence of distance responses on Leg-B).

Because the measure of model error used in Experiment 1 yielded an ambiguous solution for the variable-return data, we used an alternate measure of model error, based on the turn and distance errors rather than endpoints.[3] Table 4 shows the encoding parameters fit to each condition. As was expected, the functions for right and left turns were quite different in the variable-outbound condition and more similar in the variable-return condition. Also as expected, in the variable-outbound condition, the encoded value of Leg-A that was estimated independently was similar to an estimate based on the Leg-B encoding function. However, the two estimates were quite different in the variable-return condition. Specifically, if the 4-m Leg-A was encoded according to the Leg-B encoding functions shown in the table, the encoded value would be 3.4 m in the variable-return condition, cf. 2.8 m for the independently estimated parameter, and 3.6 m in the variable-outbound condition, cf. 3.5 m for the independently estimated parameter.

As can be seen in Figure 8, lower panels, the model accounted for the gross aspects of the data, particularly the difference in left and right turns in the variable-outbound data and the dependence of Leg-C responses on Leg-B values in the variable-return data. Correlations between the model-predicted signed error and the actual signed error, computed across paths, averaged 0.83 over the two response measures (Leg-C and Turn-2) and two

groups, and the average slope of the function relating model-predicted signed error to actual error was 0.81. It is not surprising that the model fits the data reasonably well, given the number of parameters relative to the number of observed paths. The principal value of the model here is in indicating that the nature of encoding varied considerably with the outbound-path values that the subjects experienced.

Discussion

Subjects in the two conditions in this study traced triangular paths in opposite directions, culminating in response turns of idential magnitude. Their experiences with the values of the outbound legs and turns were, as a result, quite different. The question was whether the differences would affect subjects' performance. In particular, would the difference in variability of return courses favor the variable-return group, which had more widely varying courses? Would the data indicate different encoding functions in the two groups, reflecting the differential variability in the outbound-path values they experienced?

The manipulation of course variability was directed at the issue of whether navigators represented the spatial relationships of the paths to one another and computed the response in terms of the required homeward course, resulting in interference when return courses were all similar. This is contrary to the object-centered representation assumed by the encoding-error model. There was little difference in the variable-outbound vs. return conditions with respect to return-course error (see Figure 7), despite the considerable difference in variability of the required course response. This result fails to support the idea that the return path was being represented by course.

Fit of the standard encoding-error model, which assumes that one common encoding function is applied to all leg lengths, and another to all turns, was poor. The model suggested by the data allowed for multiple encoding functions. The derived parameters indicated that subjects in the variable-outbound condition, who experienced Turn-1 values that were all quite large, differentially encoded left and right turns. It also indicated that subjects in the variable-return condition, for whom Leg-A was constant and Leg-B was variable, differentially encoded the two legs. Thus, the model indicates that by virtue of their differing experience with the distribution of path feature values, subjects adopted distinct ways of encoding the paths. We had initially hypothesized that greater variability in a parameter of the outbound path would result in a steeper encoding function, indicating that navigators differentiated among the parameter values to a greater extent. This hypothesis received little support. In fact, the slope of the leg-length encoding function was equivalent for the two groups despite differences in variability

among the outbound legs, and the slope of the turn encoding function was not consistently greater for the group having greater variability in outbound turn.

General discussion

The present paper addressed three issues. The first was whether path integration reflects experience with navigated paths. The second issue concerned a specific hypothesis about experience, namely, that it affects encoding of path features. This hypothesis therefore concerns the generality of the encoding-error model. The third issue is the nature of the path representation that subjects use. According to the encoding-error model, this representation is object-centered; it does not relate the paths to one another in terms of a common reference direction.

Relation of the encoding functions to experience with traveled paths

Initially, we considered two extreme hypotheses about the effects of experience. (i) Navigators might be unaffected by experience. A priori, we considered this unlikely. (ii) A more plausible alternative is that they assimilate responses to past experience. In that case, one can ask how much relative weight is given to the most recently experienced paths; that is, how rapidly the assimilation progresses. A strong indication of the effect of experience from past work (Loomis et al. 1993) is a tendency for the mean of subjects' responses to approach the mean of the correct values in a set of experienced paths.

Experiment 1 manipulated the region of turn and distance values represented within a block of paths, in order to determine how rapidly navigators would adapt. The question was whether navigators' responses would show separate matching to the mean within a block. In contrast to this idea, a linear function fit to the data relating responses to correct values, computed across regions, accounted for most of the variance (89%–97%), and systematic departures from linearity were not as predicted by assimilation to the local mean of a region of paramter values. Thus rapid assimilation of responses to values experienced within a single blocked set was not indicated.

The phenomenon of matching the mean of responses to the mean of correct values, and concomitant accurate responding at the mean, was not evidenced generally across these experiments. Although the condition with partial vision in Experiment 1 tended to show the most accurate responding at the mean of correct values, the no-vision condition did not. One might not

expect matching to the mean in Experiment 1, where stimulus values were blocked by region, but the phenomenon also failed to emerge in Experiment 2.

The answer to the question raised above, as to whether experience with recent paths affects path integration, appears from these data to be affirmative. However, navigators do not adapt so rapidly as to produce block by block differences under the circumstances of the present Experiment 1, nor do they necessarily assimilate mean responses to the mean of required responses.

Does experience affect encoding of path features?

To address whether experience affects the nature of encoding, we fit the linear version of the encoding-error model to the data. The hypothesis of experience-free encoding indicates that there is an immutable set of generalized encoding functions for all paths; presumably, those would incorporate the parameters derived by Fujita et al. (1993). However, the presently extracted parameters differed from previous ones and even between conditions, indicating that encoding is not immutable but rather is experience-dependent.

Although manipulations of experience affected the derived encoding functions, they did not change encoding processes as predicted. Partial vision in Experiment 1 was expected to increase subjects' sensitivity to path features, yielding a slope in the encoding function closer to 1.0 than the no-vision slope. This would, in turn, tend to increase the slope of the function relating responses to correct values for the Vision condition, relative to the No-Vision condition. Performance did improve with partial vision; however, the observed empirical effect was on the intercept of the response vs. correct function. That is, responses moved closer to the diagonal, but there was no discernable expansion of the response range when partial vision was provided, which would affect the slope of the function. Not surprisingly, then, fits of the encoding-error model did not attribute the improvement of performance with vision to increased slopes of the encoding functions. In Experiment 2, although experience with different levels of variability in path features affected performance, and those effects could be predicted by the model, the predictions that the effects would take the form of changes in the encoding-function slopes were not generally confirmed.

Object-centered representation vs. relative spatial disposition

The encoding-error model specifies one version of an object-centered representation, consisting of encoded values of leg lengths and turns. Its assumptions do not make use of a reference frame in which the spatial relationships among paths are represented. Experiment 2 showed no evidence that the

paths were anchored with respect to a common reference direction and that response course was computed, in that greatly decreased variability in return course failed to increase error. It is not surprising that whole-body navigation without vision, and without azimuthal cues or tangible landmarks, fails to make use of a reference system relating the individual paths. Among topics for future research is the extent to which azimuthal cues, such as distant sound sources, cause navigators to turn from object-centered representations, and their apparent fallibility in encoding, to externalized reference frames.

Implications for the model

The present studies expand our understanding of encoding as a basis for error in path integration. The data indicate that multiple encoding functions can be formed, reflecting experience, and multiple functions can even be applied within a single path. In this respect the simplicity of the original model cannot be maintained, and the generality of any set of empirical encoding functions is limited. The data nevertheless are consistent with the essential assumption of the model: its attribution of systematic errors in path integration, given minimal cues outside proprioception itself, to processes that encode leg-lengths and turns and that result in an object-centered representation.

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Notes

[1] In the Fujita et al., 1993, paper, the parameters of the encoding function for stimulus angle were reported in terms of the inner angle of the triangle (called alpha), not the turn made by the subject. Here we report the parameters in terms of turn, which results in a change in the intercept from 50° to 44°.

[2] We felt that the assumption of a linear encoding function may be inappropriate for the variable return condition, in which Turn-1 values were all near 180°. Accordingly, we developed a sigmoid function for turn encoding, of the form: $(2a + 1)*x^{(2a + 1)} + bx$. The function was scaled so as to pass through the points (0,0) (90,90), and (180, 180), but had a flattened middle section for a range of parameter values. Increasing the *a* parameter changes the rate of rise at the ends, and increasing *b* increases the slope in the middle section. When b:a > 2, the function is very nearly linear. Initial runs with this sigmoid on the group data combined, using the endpoint-distance error function for the model, produced an angle encoding function that

was linear with slope near 1. Therefore, we continued to use a linear encoding function for the present modeling.

[3] The difference between the empirically obtained signed error and the model-predicted signed error for a given measure (Turn-2 or Leg-C) was squared, then normalized by the s.d. of the empirical error (as computed over all paths in the condition) and then the normalized squared values were summed over all paths and both measures (Turn-2 and Leg-C).

References

Benhamou, S. and Ségunoit, V. (1995). How to Find One's Way in the Labyrinth of Path Integration Models? *Journal of Theoretical Biology* 174: 463–466.

Beritoff, J.S. (1965). *Neural Mechanisms of Higher Vertebrate Behavior* (Trans and ed., W.T. Liberson). Boston: Little, Brown.

Crowder, R.G. (1976). *Principles of Learning and Memory*. Mahwah, NJ: Erlbaum.

Dodds, A.G., Howarth, C.I. and Carter, D.C. (1983). Memory for Movement in Blind Children: The Role of Previous Visual Experience, *Journal of Motor Behavior* 15: 343–352.

Etienne, A.S., Maurer, R. and Saucy, F. (1988). Limitations in the Assessment of Path Dependent Information, *Behaviour* 106: 81–111.

Fujita, N., Klatzky, R.L., Loomis, J.M. and Golledge, R.G. (1993). The Encoding-Error Model of Path Completion Without Vision, *Geographical Analysis* 25: 295–314.

Fujita, N., Loomis, J.M., Klatzky, R.L. and Golledge, R.G. (1990). A Minimal Model for Dead-Reckoning Navigation: Updating the Homing Vector, *Geographical Analysis* 22: 326–335.

Gallistel, C.R. (1990). *The Organization of Learning*. Cambridge, MA: MIT Press.

Helson, H. (1948). Adaptation-Level as a Basis for a Quantitative Theory of Frames of Reference. *Psychological Review* 55: 297–313.

Hoffmann, G. (1984). Orientation Behaviour of the Desert Woodlouse *Hemilepistus Reaumuri*: Adaptations to Ecological and Physiological Problems, *Symposium of the Zoological Society of London* 53: 405–422.

Juurmaa, J. and Suonio, K. (1975). The Role of Audition and Motion in the Spatial Orientation of the Blind and Sighted, *Scandinavian Journal of Psychology* 16: 209–216.

Klatzky, R.L. (1999). Path Completion after Haptic Exploration Without Vision: Implications for Haptic Spatial Representations, *Perception and Psychophysics* 61: 220–235.

Klatzky, R.L., Golledge, R.G., Loomis, J.M., Cicinelli, J.G. and Pellegrino, J.W. (1995). Performance of Blind and Sighted Persons on Spatial Tasks, *Journal of Visual Impairment and Blindness* (Jan.–Feb.): 70–82.

Klatzky, R.L., Loomis, J.M., Golledge, R.G., Cicinelli, J.G., Doherty, S. and Pellegrino, J. W. (1990). Acquisition of Route and Survey Knowledge in the Absence of Vision, *Journal of Motor Behavior* 22: 19–43.

Kuipers, B. (1978). Modeling Spatial Knowledge, *Cognitive Science* 2: 129–153.

Landau, B., Spelke, E. and Gleitman, H. (1984). Spatial Knowledge in a Young Blind Child, *Cognition* 16: 225–260.

Loomis, J., Golledge, R. Klatzky, R.L., Speigle, J. and Tietz, J. (1994). Personal Guidance System for the Visually Impaired. *Proceedings of the First Annual ACM/SIGCAPH Conference on Assistive Technologies*, Marina del Rey, CA (pp. 85–91). New York: Assn. for Computing Machinery.

Loomis, J.M., Klatzky, R.L., Golledge, R.G. Cicinelli, J.G., Pellegrino, J.W. and Fry, P. (1993). Nonvisual Navigation by Blind and Sighted: Assessment of Path Integration Ability, *Journal of Experimental Psychology: General* 122: 73–91.

Marr, D. (1982). *Vision*. San Francisco: W.H. Freeman & Co.

MacEachren, A.M. (1992). Application of Environmental Learning Theory to Spatial Knowledge Acquisition from Maps, *Annals of the Association of American Geographers* 82: 245–274.

Maurer, R. (1998). A Connectionist Model of Path Integration with and without a Representation of Distance to the Starting Point, *Psychobiology* 26: 21–35.

Maurer, R. and Ségunoit, V. (1995). What is Modelling For? A Critical Review of the Models of Path Integration, *Journal of Theoretical Biology* 175: 457–475.

Mittelstaedt, H. (1985). Analytical Cybernetics of Spider Navigation. In F.G. Barth (ed.), *Neurobiology of Arachnids* (pp. 298–316). Berlin: Springer Verlag.

Mittelstaedt, M. and Glasauer, S. (1991). Idiothetic Navigation in Gerbils and Humans, *Zoologische Jahrbucher Abteilungun für Algemeine Zoologie und Physiologie der Tiere* 95: 427–435.

Müller, M. and Wehner, R. (1988). Path Integration in Desert Ants, *Cataglyphis fortis*, *Proceedings of the National Academy of Sciences* 85: 5287–5290.

Rieser, J.J. and Frymire, M. (1995). Locomotion with Vision is Coupled with Knowledge of Real and Imagined Surroundings. Paper Presented at the Annual Meeting of the Psychonomic Society, Los Angeles, CA, November 10–12.

Rieser, J.J., Guth, D.A. and Hill, E.W. (1986). Sensitivity to Perspective Structure While Walking with Vision, *Perception* 15: 173–188.

Sadalla E.K. and Montello, D.R. (1989). Remembering Changes in Direction, *Environment and Behavior* 21: 346–363.

Sauve, J.P. (1989). *L'orientation spatiale: formalisation d'un modele de memorisation egocentree et experimetation chez l'homme*. Ph.D. Thesis, Universite d'Aix-Marseille II.

Séguinot, V., Maurer, R. and Etienne, A. (1993). Dead Reckoning in a Small Mammal: The Evaluation of Distance, *Journal of Comparative Physiology A* 173: 103–113.

Sholl, M.J. (1989). The Relation Between Horizontality and Rod-and-Frame and Vestibular Navigational Performance, *Journal of Experimental Psychology: Learning, Memory, and Cognition* 15: 110–125.

Strelow, E.R. (1985). What is Needed for a Theory of Mobility: Direct Perception and Cognitive Maps – Lessons from the Blind, *Psychological Review* 92: 226–248.

Tversky, B. (1981). Distortions in Memory for Maps, *Cognitive Psychology* 13: 407–433.

von Saint Paul, U. (1982). Do Geese Use Path Integration for Walking Home? In F. Papi and H.G. Wallraff (eds.), *Avian Navigation* (pp. 298–307). Berlin: Springer-Verlag.

Wehner, R. and Wehner, S. (1986). Path Integration in Desert Ants. Approaching a Long-Standing Puzzle in Insect Navigation, *Monitore Zoologico Italiano* 20: 309–331.

Wilson, M.A. and McNaughton, B.L. (1993). Dynamics of the Hippocampal Ensemble Code for Space, *Science* 261: 1055–1058.

Worchel, P. (1951). Space Perception and Orientation in the Blind, *Psychological Monographs* 65: 1–28.

Worchel, P. (1952). The Role of the Vestibular Organs in Space Orientation, *Journal of Experimental Psychology* 44: 4010.

Yamamoto, T. (1991). A Longitudinal Study of the Development of Spatial Problem Solving Ability in the Early Blind, *Japanese Journal of Psychology* 61: 413–417.