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Updating egocentric representations in human navigation

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Abstract

Seven experiments tested whether human navigation depends on enduring representations, or on momentary egocentric representations that are updated as one moves. Human subjects pointed to unseen targets, either while remaining oriented or after they had been disoriented by self-rotation. Disorientation reduced not only the absolute accuracy of pointing to all objects ('heading error') but also the relative accuracy of pointing to different objects ('configuration error'). A single light providing a directional cue reduced both heading and configuration errors if it was present throughout the experiment. If the light was present during learning and test but absent during the disorientation procedure, however, subjects showed low heading errors (indicating that they reoriented by the light) but high configuration errors (indicating that they failed to retrieve an accurate cognitive map of their surroundings). These findings provide evidence that object locations are represented egocentrically. Nevertheless, disorientation had little effect on the coherence of pointing to different room corners, suggesting both (a) that the disorientation effect on representations of object locations is not due to the experimental paradigm and (b) that room geometry is captured by an enduring representation. These findings cast doubt on the view that accurate navigation depends primarily on an enduring, observer-free cognitive map, for humans construct such a representation of extended surfaces but not of objects. Like insects, humans represent the egocentric distances and directions of objects and continuously update these representations as they move. The principal evolutionary advance in animal navigation may concern the number of unseen targets whose egocentric directions and distances can be represented and updated simultaneously, rather than a qualitative shift in navigation toward reliance on an allocentric map.
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1. Introduction

How do people and animals represent the spatial properties of their environment so as to locate objects and navigate effectively to significant places? Research on insects suggests that one form of navigation – homing – can depend on a continuous updating process over self-motion, i.e. path integration (Srinivasan, Zhang, Lehrer, & Collett, 1996; Wehner & Srinivasan, 1981; see also Collett, 1996; Dyer, 1996). Rodents also have a path integration system that allows them to move to and from significant locations such as the nest and the site of an enduring food source (Etienne, Maurer, & Sguinot, 1996; Mittelstaedt & Mittelstaedt, 1980; for review see Gallistel, 1990). Unlike many ants and bees, however, rodents also are able to navigate to familiar objects along novel paths from novel, arbitrary points, suggesting that their spatial learning involves the construction of a qualitatively different type of spatial representation: an enduring, observer-free 'cognitive map' of the environment (e.g. O'Keefe & Nadel, 1978; Sutherland & Dyck, 1984; Tolman, 1948; for discussion see Bennett, 1996; Gallistel, 1990). Evidence for such cognitive maps gains much intuitive appeal from studies of humans. Although humans seem to have a path integration mechanism that resembles that of insects and rodents (e.g. Berthoz, Israel, Francois, Grasso, & Tsuzuku, 1995; Fukusima, Loomis, & Da Silva, 1997; Loomis et al., 1993), they also can perform diverse spatial tasks, such as imagining and drawing the furniture in a room, navigating through unfamiliar territory by means of real maps, and even charting new territory during explorations. These latter abilities suggest that real maps have a mental counterpart, and that humans and other mammals navigate by constructing and using enduring mental representations of the allocentric distances and directions of the objects and places in their environment.

In addition to behavioral evidence such as that cited above, evidence from neurophysiological experiments has been interpreted as supporting the existence of one or more cognitive maps of the environment. In particular, a variety of studies have shown that individual neurons in the hippocampus of freely moving rats are active when a rat moves through a particular region of the environment (McNaughton, Knierim, & Wilson, 1995; O'Keefe & Nadel, 1978). Although vestibular, somatosensory and visual cues are effective information for the establishment and modification of this firing pattern, the firing does not appear to rely exclusively on one or another cue, for it persists when a rat is carried passively through the environment, when visual cues are removed, and when the visual field is altered by changing the rat's facing direction (e.g. Gothard, Skaggs, & McNaughton, 1996; O'Keefe & Speakman, 1987; Quirk, Muller, & Kubie, 1990; for review see McNaughton et al., 1995). Perhaps most important, the receptive fields of different place cells and head direction cells in the same animal show internal coherence during cue manipulations (Knierim, Kudrimoti, & McNaughton, 1995; Muller & Kubie, 1987). These findings suggest that ensembles of hippocampal neurons serve as a cognitive map of the environment (O'Keefe & Nadel, 1978; Wilson & McNaughton, 1993).

Nevertheless, two quite different characterizations of mammalian navigation are compatible with the behavioral and neurophysiological evidence cited above.

According to one class of accounts (Gallistel, 1990; O'Keefe & Burgess, 1996; O'Keefe & Nadel, 1978), mammals form a representation of the allocentric locations of the significant objects and places in the environment. As they move through the environment, moreover, they maintain and update a representation of their own allocentric position and bearing using internal and external cues. Mammals then navigate to an unseen goal by combining the enduring allocentric representation of the goal position with their current assessment of their own position and orientation. From these quantities, animals compute the current egocentric distance and direction of the goal, which they then approach by dead-reckoning or piloting. On this account, mammalian navigation resembles the processes that humans use when we navigate by means of real allocentric maps.

Contrary to such accounts, humans and other mammals may navigate most accurately by means of processes that form and transform egocentric representations. On this view, mammals represent the current egocentric directions and distances of significant environmental locations. As they move or turn, they update these representations by a process of vector summation: the new egocentric positions of objects are computed by adding the objects' displacement vector relative to the animal to their previous egocentric position vectors.[1] Thus, no stable, enduring allocentric cognitive map is explicitly represented.[2] Instead, the representation of environmental locations is dynamic and transient. According to this egocentric updating account, basic processes of human navigation are quite different from the symbolic navigation processes made possible by real maps, and they are quite similar to the homing processes found in insects.

Recent studies suggest that humans do have such dynamic representations. Humans use egocentric representations of objects and scenes both in localizing and in recognizing objects (e.g. Diwadkar & McNamara, 1997; Roskos-Ewoldsen, McNamara, Shelton, & Carr, 1998; Shelton & McNamara, 1997; Sholl, 1987; Tarr, 1995; Tarr, Bülthoff, Zabinski, & Blanz, 1997; Tarr & Pinker, 1989). Moreover, humans update these representations as they move in order to recognize the scene or localize an object from a different viewpoint effortlessly (Fukusima et al., 1997; Simons & Wang, 1998; Wang & Simons, 1999). Neurophysiological studies have also shown that representations of visual space in parietal cortex are updated over intended eye movements (e.g. Duhamel, Colby, & Goldberg, 1992). The existence of these abilities nevertheless does not reveal whether human navigation depends

[1] One advantage of an egocentric map is that the information it provides can be used directly to guide self-locomotion: if one intends to move to a goal, one can directly read out its egocentric direction and distance to plan a self-movement.

[2] Combinations of the two classes of accounts also are possible. In particular, McNaughton et al. (1995) propose that object positions are represented relative to the animal's position and are updated over motion, but that both the animal's head direction and the bearings of objects are represented in geocentric (i.e. compass-point) coordinates. For present purposes, this account makes the same predictions as the purely egocentric account. It appears less plausible as an account of orientation in most humans in technologically advanced societies, however, because maintenance of an accurate compass sense has become increasingly rare in our species (see Levinson, in press).

primarily on updating an egocentric map or on updating one's position in an allocentric map.

The present research attempts to address this question through studies of human navigation. Our experiments depend on a central difference between an enduring representation and an observer-centered egocentric map that is updated continuously. Whereas both kinds of maps would allow accurate object localization from various novel points as an oriented animal moves around, the two kinds of maps should be affected differently by disorientation. If humans and animals navigate by a stable, enduring allocentric map, which itself remains the same regardless of the animal's movements, then the animal can always 'look up' the egocentric directions of each target from the same map according to its estimated self-position on the map.[3] Because disorientation disrupts an animal's estimation of its own position and orientation, fully disoriented subjects will not be able to aim with accuracy to any locations on the map. Although subjects may know, for example, that a tower is 50 strides northeast of their home, they must guess their own position and orientation at random and so will fail to compute the tower's correct egocentric direction. Once disoriented subjects have guessed their own position and heading, however, the directions in which they localize a set of objects should depend on the same cognitive map that they use when oriented. Because the relative location of multiple targets is determined by the map, not the guessed self-position, target localization by oriented and disoriented subjects therefore should show equal *internal consistency* when tested under otherwise equivalent conditions. A disoriented subject's egocentric localization of all targets should deviate from that of an oriented subject by the same vector, equal to the difference between the subject's true versus guessed allocentric orientation and position.

Contrasting predictions come from the hypothesis that humans navigate most accurately by means of an egocentric representation, updated as they move. In order to compute the new egocentric coordinates of the target locations when one moves, one has to add a common vector to each individual target vector. Unlike using an enduring map, one has to make multiple additions instead of just updating the single vector of one's own position. Therefore, the new egocentric map preserves the relative locations among different targets if and only if all target locations are updated coherently over time. When the updating process is disrupted so that such coherence is reduced (e.g. through procedures that induce a state of disorientation), the internal consistency of pointing to different targets should decrease. Without a permanent map to refer to, a disoriented subject's pointing response should show not only an overall shift but also inconsistency among different targets.

Seven experiments compared subjects' pointing in the directions of a set of unseen targets when they were disoriented versus oriented. To simplify the analysis of these experiments, the disorientation procedure focused on subjects' representa-

[3] One can also have an enduring egocentric representation (such as a 'snapshot') stored in long term memory, which can be retrieved to calculate the current object locations. Like an allocentric map, such a representation should not be affected by disorientation. The current paradigm does not distinguish these two types of enduring representations.

tions of their heading directions. Subjects turned inertially while maintaining a constant position within the chamber. We assumed that this procedure would lead subjects to make random assessments of their heading, which in turn would produce a global shift in pointing to all targets. If subjects pointed to the targets by means of an enduring cognitive map, then disorientation should not perturb the internal angular relationships among targets. In contrast, if subjects pointed to the targets using dynamic egocentric representations maintained by continuous updating, then disorientation should impair the updating process and produce an increase in configuration error.

2. Experiment 1

In this experiment, subjects pointed to six targets first with their eyes open, then blindfolded after a small rotation, and finally blindfolded after disorientation. The initial eyes-open condition provided a measure of the represented target locations by each subject. The first eyes-closed condition served as a measure of pointing accuracy without vision in a state of orientation, after updating for a small rotation. The final disorientation condition, in which the subjects pointed to the targets immediately after an extended process of self-rotation that induced a state of disorientation, tested whether the accuracy of the angular relationships among the target objects decreased after the subjects were disoriented.

2.1. Method

2.1.1. Subjects

The participants were ten Cornell undergraduate students who were recruited from psychology classes. They received course credit for their participation.

2.1.2. Apparatus

Testing took place within a $1.9 \times 1.9 \times 2.0$ m chamber located in a larger experimental room. The walls and ceiling of the chamber were covered with white, thick, soft fabric stretched onto a concealed wooden frame. The floor was covered with a homogeneous gray carpet. A 1.9×2.0 m red satin fabric was attached with Velcro to one of the four walls, which it then covered completely. The chamber was accessed through a 0.7×2.0 m door in the wall opposite to the location of the red wall, as shown in Fig. 1. The fabric covering the door also could be secured with Velcro, such that the white walls looked identical when the door was closed. One 40 W light was placed on the ceiling in the middle of each wall to illuminate the chamber. A video camera was mounted at the center of the ceiling providing an overhead view of the chamber and sending the image to a VCR outside the chamber. Six objects – a TV, a table, a baby chair, a pile of fabric, a bookshelf and the door of the chamber – stood outside around it and were invisible from inside. The objects were arranged in an irregular configuration, such that no object stood directly at a corner or center of a wall. A tape recorder announcing the names of the targets and producing white noise

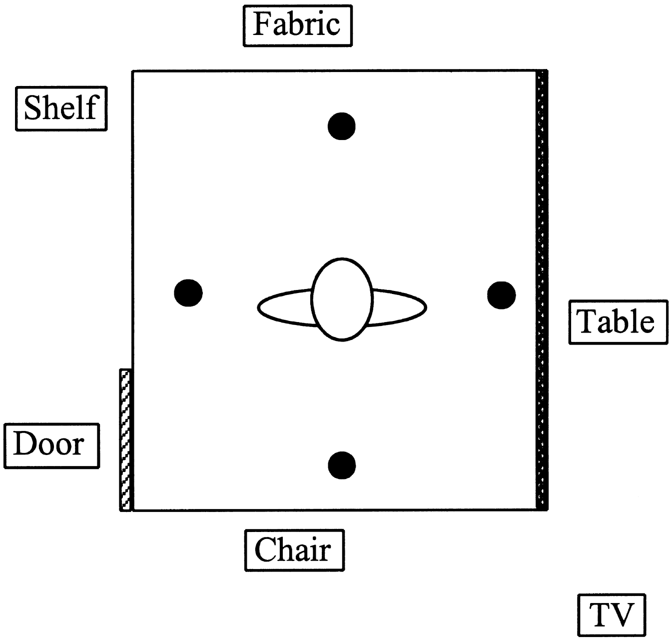

Fig. 1. An overhead view of the experimental chamber and surrounding target objects for Experiments 1–5.

during the intervals was carried by the experimenter moving about the chamber to eliminate any fixed auditory directional cues.

2.1.3. Procedure

Each subject was tested individually. The subject first was shown the six objects outside of the chamber and was asked to study the objects and remember their locations as accurately as he or she could. Subjects walked around the chamber and studied the objects from various viewpoints, taking as long as they wanted to learn the locations, and then they went into the chamber with the experimenter and stood in the middle of the room. They were asked to point to the six objects as the experimenter named them. If a subject made a mistake, he or she was asked to go outside the chamber and study the objects again. After successfully completing this initial pointing test, subjects were asked to face a randomly determined orientation, and to point to the direction of each (now invisible) target object, with whichever hand was convenient, as announced on a tape recording in a random sequence, each announcement lasting 2 s (eyes-open condition). Each subject pointed to each object four times, for a total of 24 pointing responses. Then the experimenter blindfolded the subjects and turned them to face a different orientation randomly determined. The subjects again pointed to the objects as announced (eyes-closed condition). Then the subjects were disoriented by turning around by themselves for 1 min without opening their eyes while standing in the chamber. Although some subjects changed position in the chamber slightly during the rotation, they were guided by the experimenter to the center of the chamber, while facing in the same direction, after they stopped rotating, and they were told they had returned to the center. After the subjects stopped rotating, they were allowed to remain facing in their current direction for 5 s and then were asked to point to the objects as accurately as they could, as each object was named on the tape recording (disorientation condition).

The subjects stood during each condition and then changed facing orientation at the start of a new condition. For each condition and subject, facing direction was predetermined and pseudo-randomized among the eight directions (four corners and four walls) so that each condition had a different facing direction.[4] The experimenter moved continuously inside the chamber during each condition so as not to serve as a directional cue.

2.1.4. Coding and data analysis

All coding was performed off-line from the overhead TV image. A transparent angular coordinate system, specifying all directions in 10° units, was superimposed on the TV image to facilitate measurement of the direction of each pointing response and the facing direction.

We first calculated the mean direction of the pointing responses to each object in the initial eyes-open condition. This was taken as the *represented direction* of that target for that subject. The *individual error* was the mean difference between the pointing responses to each object in each of the following conditions and the *represented direction* of that object. This indicated how many degrees each object was 'moved' from its original direction. The mean of the six individual errors in each condition therefore measured the degree of displacement in the subject's assessment of his or her own heading (*heading error*), which should be small when the subjects were oriented and be randomly distributed on the circle when they were disoriented. Whether the subjects were disoriented or oriented during a given condition was then tested using the χ^2 test described by Batschelet (1981).[5] The principal measure of interest was the *configuration error*, which indicates the accuracy of the localization of each target in relation to the others. The configuration error was defined as the standard deviation of the six individual errors, which would be zero if all six targets moved by the same amount and would be higher if they were out of phase.

Finally, the standard deviation of the successive pointing responses to the same

[4] During piloting, we rotated the subjects to another pseudo-random orientation after disorientation. However, we soon discovered that since the subjects knew nothing about which direction they were facing, it made no difference whether or not they were rotated to a predetermined orientation. In the actual experiments, therefore, we randomized the facing direction in the eyes-open and eyes-closed conditions, and the disoriented subjects faced a random orientation as a consequence of the procedure itself.

[5] For this test, we divided the circle into six equal-sized regions of 60° each, and counted the number of subjects whose overall rotations fell into each region. If the overall rotations were randomly distributed around the circle, then each region should have the same number of subjects whose overall rotation fell in that region. Any deviation from that distribution, if significant by a χ^2 test, indicates a non-random distribution, which implies that subjects are oriented or mis-oriented systematically.

target in each condition was calculated and averaged across six targets to measure the variability of repeated pointing responses to a single target (*pointing error*). The measured pointing error was then used to correct for pointing variability in assessing subjects' configuration error (as described in Section 3.3). Subjects' ability to remember the ordinal relationship among the targets also was assessed by comparing the clockwise sequence of the six objects in the first eyes-open condition with that in each of the subsequent conditions.

2.2. Results

2.2.1. Heading error

The upper panel of Fig. 2 presents the errors in the represented facing directions for each subject during the eyes-closed and disorientation conditions. Although the facing directions represented by subjects were quite accurate in the eyes-closed

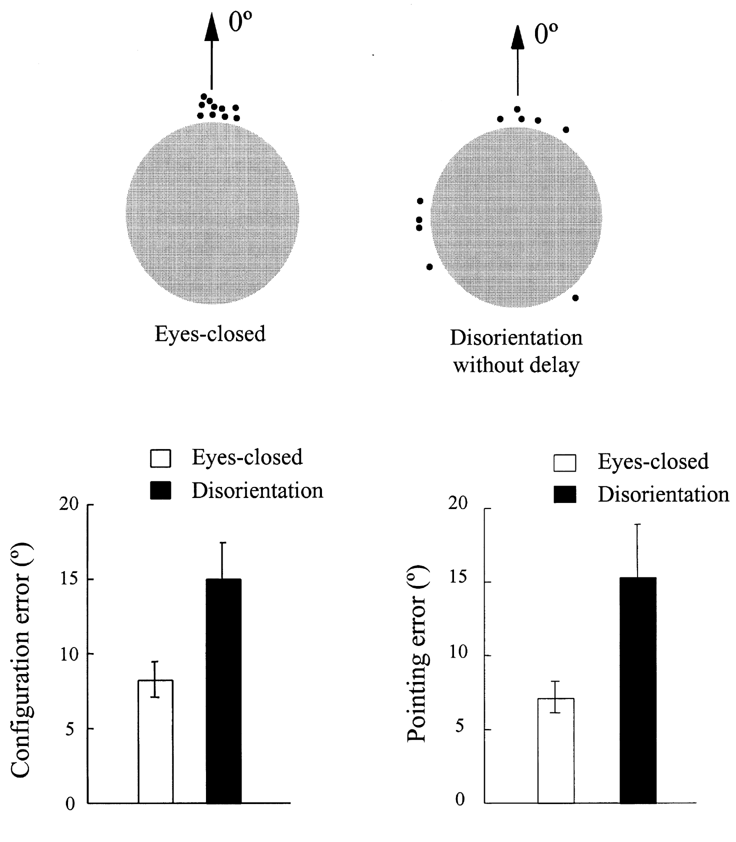

Fig. 2. The heading error, configuration error and pointing error in Experiment 1. The top panels show the heading error in the eyes-closed and disorientation-without-delay conditions. Each dot represents the heading error of one subject. The lower left panel shows the configuration error and the lower right panel shows the pointing error. The error bars are standard errors.

condition ($\chi^2(5) = 50.0$, $P < 0.0001$), those represented by subjects after disorientation were random ($\chi^2(5) = 6.8$, $P > 0.24$). These findings indicate that subjects' sense of orientation was preserved with eyes closed but was fully disrupted by the disorientation procedure.

2.2.2. Configuration error

The lower left panel of Fig. 2 presents the internal consistency among the pointing responses to different objects in the two test conditions. The configuration error is significantly higher in the condition that immediately followed disorientation than in the eyes-closed condition ($t(9) = -2.39$, $P < 0.05$). All ten subjects gave the correct clockwise sequence of the six targets in both conditions.

2.2.3. Pointing error

The lower right panel of Fig. 2 presents the variability of pointing to individual targets in each test condition. There was a marginally significant increase in response variability in the condition that followed disorientation, relative to the preceding eyes-closed condition ($t(9) = 2.13$, $P = 0.06$). The relation of configuration errors to pointing errors is discussed and analyzed further in Experiment 2.

2.3. Discussion

The subjects showed a significant decrease in the internal consistency among target locations after they were disoriented. This provides initial evidence that their representation of object locations relied on their assessment of their own orientation. Without an accurate sense of their own direction in a given environment, subjects may have had difficulty localizing objects in the environment coherently and accurately. Such difficulty, in turn, implies that object localization did not depend on an enduring cognitive map but on egocentric representations and updating processes.

There are, however, two classes of alternative accounts for the increase in configuration error after disorientation. First, subjects' representations of the environment may be impaired, but not because of their loss of a sense of their own orientation per se. In particular, subjects' configuration error might be increased because errors in the representations of the positions of individual targets accrued as a result of the passage of time or the activities used to produce disorientation. Second, disorientation may leave subjects' representations of the environment intact but impair their performance for other reasons. For example, the increase in configuration error might be due to the decreased accuracy of the pointing response after self-rotation. Self-rotation may cause vestibular stimulation and somatosensory disturbance, impairing subjects' ability to point in the directions where they represented the targets. As a second example, the increase in configuration error might stem from disoriented subjects' representation of a change in their position as well as their orientation. If subjects pointed at targets from a new represented position, then the angular relations among targets should change, even if the cognitive map itself was unaffected. Finally, a disoriented subject may constantly vary his or her guessed orientation, and combine his or her cognitive map with different guesses of self-orientation for each target. This inconsistency in retrieval can lead to inconsistency in successive pointing responses even though the cognitive map itself is intact.

To determine whether subjects' inaccuracy in the disorientation condition stemmed from a deficit in motor control, a change in their sense of position in the chamber, an increase in localization errors due to the passage of time or the disorientation procedure, or the loss of a sense of orientation, we further tested the phenomenon in four experiments. In Experiment 2, we introduced a 30 s delay after self-rotation to permit recovery from the possible vestibular and somatosensory fatigue. In Experiment 3, we directly compared spatial memory retrieval with a simple motor guidance task. To minimize any changes in perceived self-position produced by the disorientation procedure, the subjects in Experiment 2 sat in a swivel chair fixed to the floor, such that their position remained constant as they turned (the effects of possible variations in perceived self-position in the swivel chair were also tested further in Experiments 4 and 5). Finally, in Experiments 4 and 5, we compared the configuration error of subjects who participated in identical activities, for identical delays, and under identical procedures, with or without a directional visual cue to preserve their sense of orientation.

3. Experiment 2

In Experiment 2, subjects participated in the same three conditions as in Experiment 1, with two changes in procedure. First, subjects were seated throughout the experiment in a swivel chair at a fixed position but variable orientation, in order to minimize the possibility that they would perceive their position to change over the course of the study. Second, subjects were given a 30 s recovery period after the disorientation procedure and before the final pointing test, so as to allow their vestibular system to recover from the effects of the disorientation procedure itself. If the increase in configuration error observed after disorientation in Experiment 1 was caused by effects of the disorientation procedure on subjects' representation of their position or by direct effects of that procedure on the vestibular and proprioceptive systems, then this increase should be smaller in Experiment 2. In contrast, if the increase in configuration error stemmed from the effect of disorientation per se, then the same increase should occur in Experiment 2.

3.1. Method

The participants were ten Cornell summer school students who volunteered for the experiment. The subjects sat in a swivel chair with a rotatable seat that stood in a fixed location at the center of the chamber. For the disorientation procedure, subjects turned while sitting in the chair by pushing against the floor with their feet for 1 min. Subjects pointed to each target twice in each of the three conditions, for a total of 12 pointing responses/condition. The method was otherwise the same as in Experiment 1.

3.2. Results

As shown in the top panel of Fig. 3, subjects showed little heading error with eyes closed, indicating that they maintained an accurate sense of orientation ($\chi^2(5) = 50.0$, $P < 0.0001$). In contrast, subjects showed large and random heading errors after the disorientation procedure, indicating that they were disoriented ($\chi^2(5) = 2.00$, $P = 0.85$).

As shown in the lower left panel of Fig. 3, the configuration error increased in the disorientation condition, compared to the previous condition in which subjects pointed with eyes closed in a state of orientation ($t(9) = 2.65$, $P < 0.05$). Three of the ten subjects made at least one error on the ordinal sequence of the six targets in the disorientation condition, whereas no subject made such an error in the eyes-closed condition.

The lower right panel of Fig. 3 presents the mean SD of the pointing responses to individual objects in the two test conditions. Pointing errors were significantly

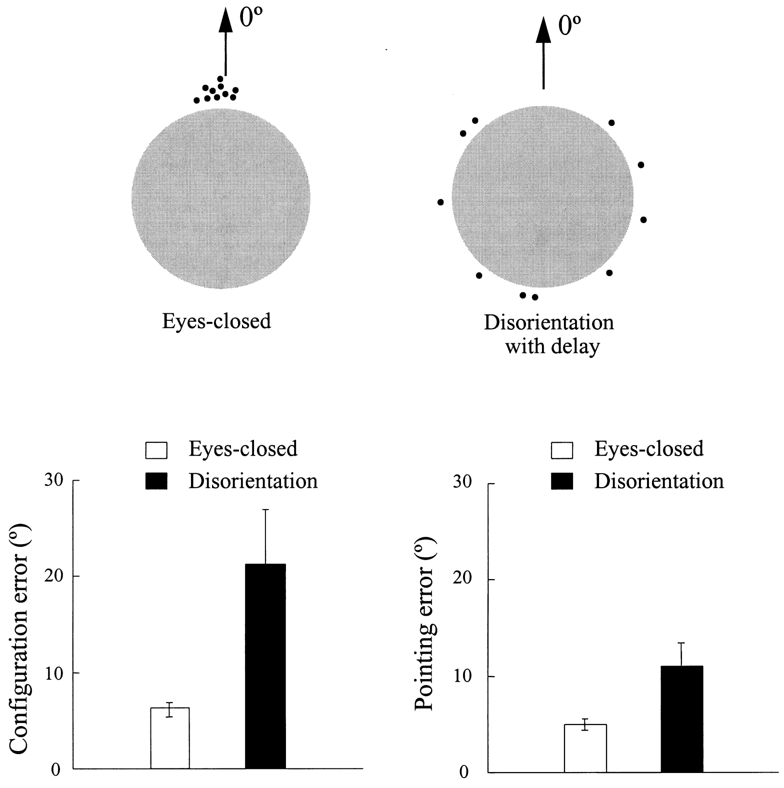

Fig. 3. The heading error, configuration error and pointing error in Experiment 2. The top panels show the heading error in the eyes-closed and disorientation-with-delay conditions. Each dot represents the heading error of one subject. The lower left panel shows the configuration error and the lower right panel shows the pointing error. The error bars are standard errors.

higher in the disorientation condition than in the eyes-closed condition ($t(9) = 2.43$, $P < 0.05$).

3.3. Discussion

The subjects in Experiment 2 showed large heading errors after the disorientation procedure, indicating that rotating on a fixed chair was as effective at disorienting the subjects as was standing and turning. Moreover, the subjects showed a significant increase in configuration error in the disorientation condition, despite the use of a fixed chair and the introduction of a 30 s recovery period between the disorientation procedure and the pointing test. This finding suggests that the increase in configuration error does not stem from a change in subjects' representation of their own position or from the direct effects of disruption to the vestibular system caused by the disorientation procedure itself. Further evidence for this conclusion will be presented in Experiment 4.

In both Experiments 1 and 2, subjects showed an increase in the mean SD of repeated pointing responses to individual targets: they were less consistent in pointing to the same object after they were disoriented. This increase may reflect the general uncertainty of where the targets were when the subjects were disoriented, or stem from their uncertainty of their own heading: if subjects were not sure about their heading, they could vary their best guesses from one pointing response to another, causing more variability in pointing to the same target at a different time, and altering the configuration of their pointing to different targets. Thus, due to

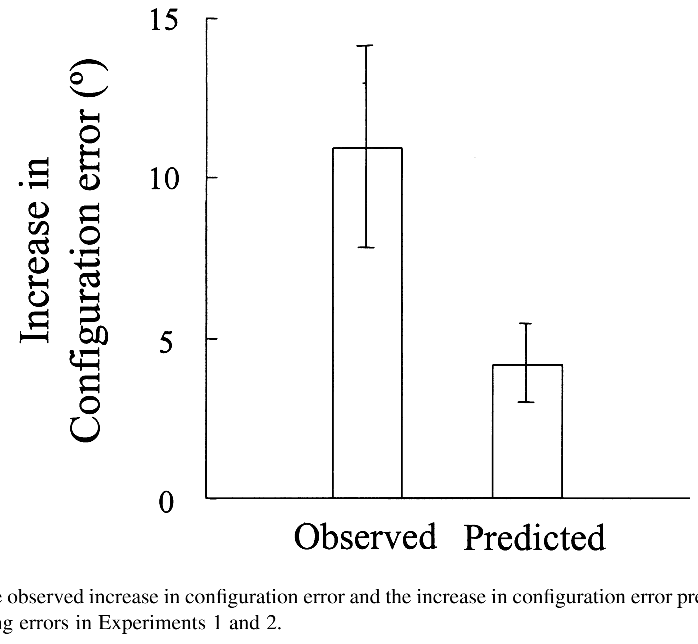

Fig. 4. The observed increase in configuration error and the increase in configuration error predicted from the pointing errors in Experiments 1 and 2.

inconsistent retrieval one can show increased configuration error even with an accurate cognitive map. This hypothesis was tested in Experiments 4 and 5.

3.3.1. Increase of configuration error due to increase of pointing error

Higher variability in the pointing responses can itself cause an increase in configuration error, even if pointing responses are guided by an enduring and accurate cognitive map. If the increased variability in pointing responses is the sole cause of the increase of configuration error, the magnitude of the increase in configuration error can be predicted from the increase in pointing error on statistical grounds. We tested this relationship, assuming homogenous variance of the pointing responses to all targets and independence of each pointing response. Since the mean of N pointing responses is likely to be off by the standard deviation of the N pointing responses divided by the square root of N, therefore

$$\text{Predicted increase in configuration error} = \frac{\text{Increase in pointing error}^{6}}{\sqrt{N}}$$

Since there was no significant difference in the disorientation conditions between the two samples ($t(18) = 0.98$, $P = 0.34$), we combined the data from Experiments 1 and 2, as shown in Fig. 4. The observed increase in configuration error after disorientation was significantly higher than that predicted from the increase in pointing errors ($t(19) = 2.24$, $P = 0.03$). Therefore, the increase in configuration error after disorientation appears to be more than just an artifact of the increased variability of subjects' responses. However, it remains possible that some of the statistical assumptions required for the present analysis may not hold (see footnote 6). Experiments 4 and 5 further tested the cause of the increased configuration error after disorientation by manipulating a directional cue during self-rotation.

In summary, Experiment 2 provides evidence that disorientation itself, and not the after effects of the disorientation procedure on the vestibular system, leads to an increase in the configuration error, in accordance with the egocentric updating hypothesis. Nevertheless, it may take longer than 30 s for the vestibular and proprioceptive systems to recover from the disorientation procedure. In addition, factors such as fatigue or declining motivation may interact with the disorientation procedure to produce a decrease in pointing accuracy. In Experiment 3, therefore, we further tested the accuracy of the pointing response after the same procedure in a

[6] Note that a similar equation relating the degree of configuration error to the degree of pointing error within a single condition evidently is not valid, because the configuration error was significantly larger than the equation predicts for the eyes-closed condition. Several factors could have led to the configuration errors but not pointing errors. For example, due to biomechanical constraints and distortion of the videotaping device, subjects' pointing configuration ought to differ by a small amount in the control condition relative to the eyes-open condition, because subjects faced a different orientation. Those factors will not affect pointing consistency to the same target, because subjects maintained their orientation within a condition. Here we assume that these factors affect configuration errors in the disorientation condition to the same extent as in the control condition. Therefore, the statistical relationship holds for the increase of configuration error and the increase of pointing error.

task that required accurate motor control but no memory for the spatial directions of objects.

4. Experiment 3

In Experiment 3, subjects pointed to body-centered orientations (e.g. 'to the *right*') rather than to the target objects in the environment (e.g. 'to the *table*') under conditions that closely paralleled those of the preceding experiments, and the consistency of different pointing responses was compared when subjects were oriented versus disoriented. If the disorientation procedure directly affected subjects' motor control but not their spatial memory, then the subjects in Experiment 3 should show the same impairment in pointing consistency as those in Experiments 1 and 2. In contrast, if the disorientation procedure impaired subjects' memory for the relationships among the target objects, then the subjects in Experiment 3 should not show this impairment.

4.1. Method

The participants were eight Cornell undergraduate students who were recruited and compensated as in Experiment 1. Each subject pointed four times in each of six directions in each of three conditions (24 pointing responses/condition), as in Experiment 1. In order to provide the same number and arrangement of targets as in the spatial memory task in the first two experiments, we randomly chose six egocentric directions (front, back, right, left front, left back, right back) for this pointing task. To assure that the subjects were disoriented, they were asked after the disorientation condition to judge their facing direction by pointing to one of the target objects before the experimenter removed the blindfold. All other features of the experiment were the same as in Experiment 1.

4.2. Results

Because the primary task did not involve pointing to external targets, the heading error could only be estimated from the single, final trial in which the subject pointed to a target after disorientation, by subtracting the pointing direction from the true direction of the target. Performance on this trial revealed that the subjects were effectively disoriented ($\chi^2(5) = 5.50$, $P = 0.36$), as shown in the top panel of Fig. 5.

The lower left panel of Fig. 5 presents the configuration error, again measuring the internal inconsistency of pointing in different directions, in the eyes-closed and the disorientation conditions. The subjects showed a slight decrease in configuration error in the disorientation condition, an effect opposite to that predicted by the thesis that disorientation causes general decrement in pointing accuracy. There was no significant difference in configuration error across the test conditions before and after disorientation ($t(7) = -0.61$, $P = 0.56$). As indicated in the lower right panel of Fig. 5, the mean pointing error also showed no significant difference across the two conditions ($t(7) = 0.11$, $P = 0.92$).

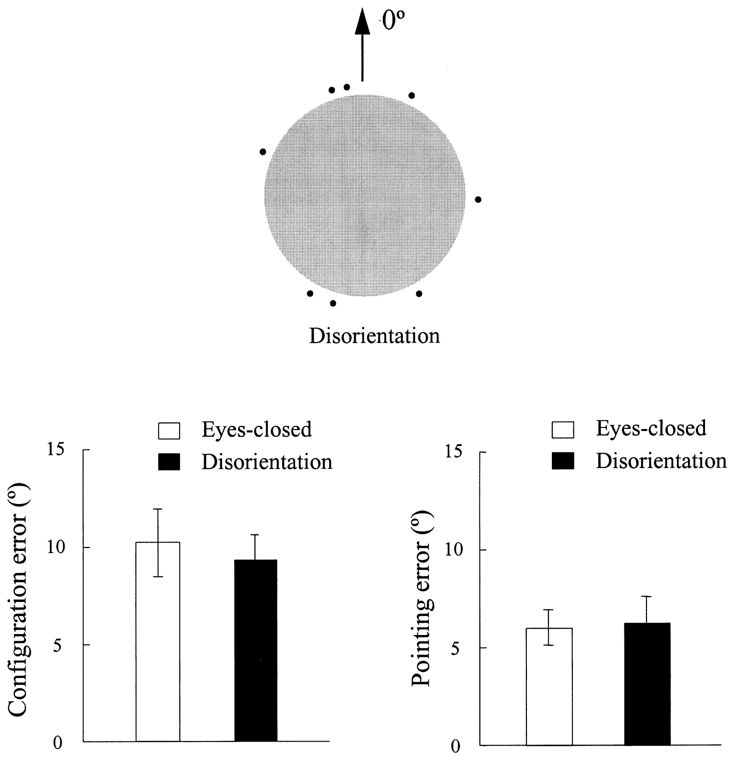

Fig. 5. The heading error, configuration error and pointing error in Experiment 3. The top panel shows the heading error in the disorientation condition. Each dot represents the heading error of one subject. The lower left panel shows the configuration error and the lower right panel shows the pointing error. The error bars are standard errors.

4.3. Discussion

Subjects pointed to different egocentric directions with equal consistency, regardless of whether they were oriented or disoriented. This finding, in conjunction with the findings of Experiments 1 and 2, provides evidence that the disorientation process interfered with spatial memory, not with the pointing response. Motor control accuracy without visual guidance may be responsible for part of the variation in repeated pointing responses in both the eyes-closed and the disorientation conditions, but it cannot account for the increase in configuration error observed in the disorientation conditions of Experiments 1 and 2.

The disorientation procedure has three consequences. It physically stimulates the vestibular system, which has been shown to be important for many spatial tasks, it occupies time and requires that subjects engage in potentially interfering spatial activities, and it causes the subjects to lose their sense of orientation. Which aspect of the rotation caused the increase in configuration error? If this increase is due to the physical stimulation of the vestibular system, or to the impairment of spatial memory caused either by the passage of time or by the action of turning, we should observe an increase in configuration error whenever people go through a self-rotation procedure, regardless of whether or not they are disoriented. If this increase is due to subjects' loss of their sense of orientation, in contrast, then the increase in configuration error should not occur if the subjects experience the same physical stimulation in the presence of a directional cue that allows them to maintain their sense of orientation. Experiment 4 tested these contrasting predictions by presenting a single light as a directional cue to orientation during the self-rotation procedure.

5. Experiment 4

In Experiment 4, subjects were given the same pointing task for the same three conditions as in Experiment 2. They pointed to external targets with eyes open, with eyes closed after a small rotation, and with eyes closed after the extensive rotation that was used in Experiments 1–3 to induce a state of disorientation. In the present experiment, however, subjects were tested with a blindfold that was translucent rather than opaque, through which a single asymmetrically placed light produced a detectable brightness gradient. Although subjects could not see either the targets or any other features of the room, the brightness gradient allowed them to assess their orientation throughout the study. If the increase in configuration error observed in Experiments 1 and 2 stemmed from factors such as the passage of time and the presence of vestibular stimulation, then the same increase should be observed in Experiment 4. In contrast, if that increase was a direct effect of disorientation, then it should not occur in the present study.

5.1. Method

The participants were ten Cornell summer school students who were recruited as in Experiment 2. Subjects were tested following the procedures of Experiment 2, with the following changes. Three of the four overhead lights in the chamber were extinguished. A single directional light therefore was present throughout the study and allowed subjects to see the direction of the one remaining light source and a brightness gradient in the chamber but no other room features. After the initial eyes-open condition, all testing took place with subjects wearing a translucent blindfold. For the initial eyes-open condition, subjects were turned by the experimenter to face the directional light, and they pointed to each target twice in a random sequence. Then they put on the translucent blindfold, were turned about 20–30° to the left or right, and pointed to the targets again (eyes-closed condition). Finally, subjects turned in the chair exactly as in Experiment 2. When they stopped, the experimenter again turned the subjects to face about 20–30° to the right or left side of the directional light and they pointed to the targets again (oriented-rotation condition). This manipulation facilitated subjects' perception of the light through the blindfold. Half of the subjects turned left in the eyes-closed condition and right in the disorientation condition, and others did the reverse.

5.2. Results

Fig. 6 (top panel) presents the heading errors for each subject in the eyes-closed and oriented-rotation conditions of the experiment. Errors were small in both eyes-closed and oriented-rotation conditions, indicating that subjects were well oriented in both conditions ($\chi^2(5) = 50.0$ and 29.6, respectively, $P < 0.0001$).

The lower left panel of Fig. 6 presents the mean configuration error in each of the two test conditions. In contrast to Experiments 1 and 2, the configuration error decreased non-significantly in the condition that followed self-rotation compared to the eyes-closed condition ($t(9) = 0.99$, $P = 0.35$), an effect that is opposite to that predicted by an effect of physical rotation on configuration error. As indicated in the lower right panel of Fig. 6, the pointing error also slightly decreased in the condition after rotation ($t(9) = 1.08$, $P = 0.31$).

5.3. Discussion

Although subjects received the same vestibular stimulation from the same self-

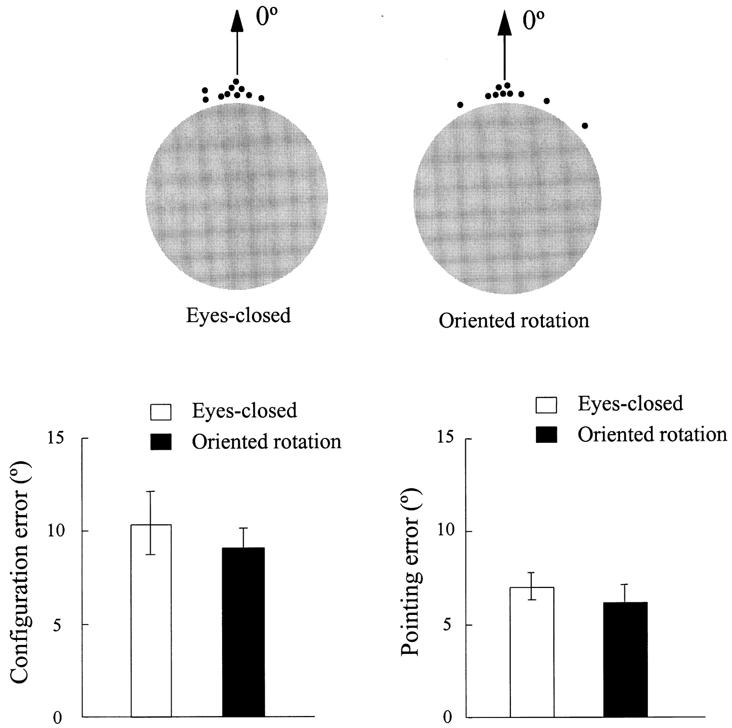

Fig. 6. The heading error, configuration error and pointing error in Experiment 4. The top panels show the heading error in the eyes-closed and oriented-rotation conditions. Each dot represents the heading error of one subject. The lower left panel shows the configuration error and the lower right panel shows the pointing error. The error bars are standard errors.

rotation procedure as in the previous experiments, they showed only small heading errors after the procedure. This finding indicates that subjects were able to use the light as a directional cue to maintain their sense of orientation. More important, subjects' configuration error was as low in the test condition that followed this procedure as in the test condition that preceded it. This finding casts light on the findings of Experiments 1 and 2. It provides further evidence that it is the disruption of one's sense of orientation that causes an increase in the configuration error, rather than either a disruption of vestibular inputs per se or an impairment in memory due to the delays or activities involved in the disorientation procedure. The experiment also provides further evidence that the increase in configuration error after disorientation does not stem from the effect of self-rotation on subjects' sense of their own position, because the directional light provided little information about one's position in the chamber (see also Experiment 5). Therefore, the accuracy of the representation appears to depend on subjects' sense of orientation, in accordance with the egocentric updating hypothesis.

If egocentric representations are continuously updated over self-motion, why was there no detectable increase in error when subjects pointed to objects after rotating in the presence of a directional signal that maintained their sense of orientation? We suggest two possible explanations. First, the dynamic updating process maybe highly accurate when subjects have access to accurate information about their own orientation: accurate enough that ten rotations are insufficient to produce detectable error. Second, the dynamic updating process may be engaged only at certain points within a period of rapid rotation rather than continuously. For example, oriented subjects may update the egocentric directions of objects only once after each complete rotation, when their displacement vector returns to zero, until the end of the rotation sequence. Desert ants appear to rely on a process of the latter kind, for they use the sun and other directional signals to calculate their orientation vector after turning too rapidly for any continuous updating process (e.g. Müller & Wehner, 1988; Wehner, 1994). Further research using the present paradigm and varying the number or speed of rotations would be needed to distinguish these possibilities. In any event, the contrast between subjects' accurate pointing in Experiment 4 and their inaccurate pointing in Experiments 1 and 2 suggests that it is the disorientation process, and not other features of the rotation procedure, that impairs accurate localization of objects, in accordance with the dynamic egocentric map hypothesis.

Nevertheless, all the findings reported so far are consistent with the contrary hypothesis that human navigation depends on an enduring cognitive map whose use is impaired when the navigator is disoriented for either of two reasons. First, it is possible that the cognitive map becomes temporarily inaccessible during disorientation: humans may have an accurate cognitive map of the environment, but they can only use this map when they can specify their own position and heading on it. When subjects are disoriented, therefore, their enduring cognitive map will not be accessible to guide their navigation. Second, it is possible that disoriented subjects locate objects by means of an accurate and stable cognitive map, but that their egocentric localization of different targets is inconsistent because they intermittently experience changes in their own perceived or guessed orientation. If disoriented subjects constantly vary their guessed or perceived heading throughout a condition, this variation will produce distortions of their pointing configuration to different targets, even if the underlying map is intact. On either of these views, the increase of configuration error occurred at the retrieval stage, rather than during the disorientation process as predicted by the egocentric updating hypothesis.

The next experiment was undertaken to distinguish the above hypotheses from the hypothesis that humans navigate by updating egocentric representations, by investigating whether information about the correct relationships among objects is recoverable after a subject's global orientation is reestablished. According to the egocentric updating hypothesis, navigation requires that a representation of environmental locations be actively maintained, and so any impairment to this representation caused by disorientation must be permanent. According to the cognitive map hypothesis, navigation depends on a representation of environmental locations that endures independently of the subject's own position or motion, and so any impairment to performance after disorientation should be transitory, caused by the temporary inaccessibility of the representation or by the unfavorable retrieval situation. If subjects are disoriented and then reoriented, therefore, the egocentric updating hypothesis predicts that they will continue to show an increase in configuration error, whereas the cognitive map hypothesis predicts that this increase will not occur.

6. Experiment 5

In Experiment 5, subjects were tested under identical conditions to those of Experiment 4, with one exception. Although they wore a translucent blindfold and were trained and tested with a single, asymmetrically placed light, the light was extinguished during the rotation procedure that preceded the final pointing condition and then re-illuminated for that condition. Therefore, subjects lost their sense of orientation during the disorientation procedure, but they reoriented themselves before the pointing test. If humans navigate accurately by means of an enduring map that is accessible and can be retrieved in a consistent manner only when they are oriented, then the subjects in Experiment 5 should have shown both accurate and consistent pointing after disorientation. In contrast, if humans navigate accurately by means of a dynamic egocentric map, then the subjects in Experiment 5 should have pointed with smaller heading errors than in Experiments 1 and 2 but with as large a configuration error as in those experiments. Although the reintroduction of the light should correct for the global error, it could not restore the dynamic, egocentric representation of target positions that was impaired during disorientation.

6.1. Method

Ten subjects from the same population as those in Experiment 4 were tested. The procedure was exactly the same as in Experiment 4, except that the light was turned off after the subjects began the rotation, and it was turned on again after the subjects stopped turning. The final pointing test was given 30 s after the light was turned on.

Thus, subjects became disoriented during the turning procedure and were given time to reorient by the light before the last pointing test.

6.2. Results

The upper panel of Fig. 7 presents the heading errors for each subject in the two test conditions of the experiment. Overall rotations were small in both the eyes-closed condition and the reorientation condition. In both conditions, subjects showed an accurate sense of orientation, as in Experiment 4 ($\chi^2(5) = 39.2$ and 29.6, respectively, $P < 0.0001$).

The lower left panel of Fig. 7 presents the configuration error in the two test conditions. Configuration error was significantly higher in the reorientation condition than in the preceding eyes-closed condition ($t(9) = 4.0$, $P < 0.005$). There was no significant difference in pointing error between the two conditions ($t(9) = 1.4$,

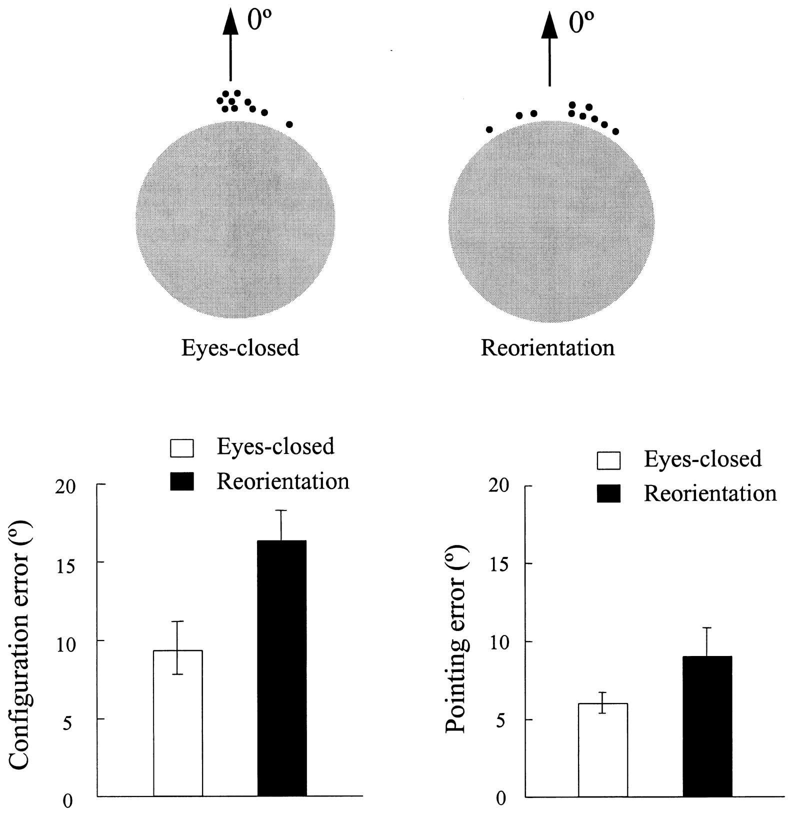

Fig. 7. The heading error, configuration error and pointing error in Experiment 5. The top panels show the heading error in the eyes-closed and reorientation conditions. Each dot represents the heading error of one subject. The lower left panel shows the configuration error and the lower right panel shows the pointing error. The error bars are standard errors.

$P = 0.20$; see the lower right panel of Fig. 7). The increase of configuration error significantly exceeded that predicted by the increase in pointing errors ($t(9) = 5.5$, $P < 0.005$). In both conditions, all subjects gave the correct clockwise ordering of the targets.

Comparing the reorientation condition in Experiment 5 to the disorientation condition in Experiment 2, there is no significant difference in configuration error ($t(18) = 0.80$, $P = 0.43$). In contrast, the configuration error was significantly higher in the reorientation condition in Experiment 5 than in the oriented-rotation condition in Experiment 4 ($t(18) = 3.5$, $P < 0.003$). There was no significant difference among the preceding eyes-closed conditions in the three experiments ($F(2, 27) = 2.0$, $P = 0.15$).

6.3. Discussion

The single light introduced after the disorientation procedure of this experiment effectively corrected subjects' heading error but not their configuration error. Although exposure to a single light source allowed subjects to correct for their overall sense of orientation, this directional cue did not contain sufficient information to enable subjects to recover the relative directions of the target objects. The representation therefore was as erroneous after reorientation (in Experiment 5) as it was in a state of disorientation (in Experiments 1 and 2), even though the global orientation had been corrected. These data provide evidence against the thesis that object localization depends on an enduring cognitive map that is made inaccessible by disorientation. More generally, these data suggest that the increase of configuration error after disorientation in Experiments 1 and 2 was not a result of the retrieval stage, but a result of the updating stage. For example, if the main cause of the increase of configuration error in Experiments 1 and 2 was due to a retrieval strategy of guessing one's heading inconsistently from trial to trial, such increase should not occur in Experiment 5, because the directional light provides information about the subjects' heading and they did not have to make guesses. The increase in pointing error in the disorientation condition of Experiments 1 and 2 may well have been caused by such a guessing strategy, because no such increase was obtained in Experiment 5. Nonetheless, the configuration errors increased in Experiment 5 as reliably as in the previous experiments, suggesting that the source of configuration error was from the disorientation period, not the testing stage afterwards.

In Experiments 4 and 5, subjects engaged in identical activities were tested in identical situations for both control and test conditions, with identical directional cues. However, when the directional cue was present throughout the experiment, the pointing configuration was preserved. When the directional cue was absent between test and control conditions while the subjects were in motion, such configuration was impaired. The critical component for an accurate representation of object locations appears to be continuous knowledge of one's own orientation, suggesting that people rely on an egocentric map that is continuously updated from the previous one. Such a representation appears to be irreversibly impaired by disorientation, which defeats the continuous updating process.

Although Experiments 1–5 provide evidence that object locations are represented egocentrically through a dynamic updating process, they do not show that all spatial information is represented in this manner. In particular, it is possible that the shape of the surrounding surface layout itself is captured by an enduring representation. Various studies have shown a fundamental difference in spatial representations of object locations and environment geometry (e.g. Cheng & Gallistel, 1984; Epstein & Kanwisher, 1998; Hermer & Spelke, 1994, 1996; Shelton & McNamara, submitted for publication). For example, Cheng and Gallistel (1984) showed that disoriented rats used the shape of a box to locate hidden food, but that they failed to use non-geometric cues such as the brightness of the wall, visual patterns of the corner, and odors. Young children showed a similar behavior pattern when disoriented (Hermer & Spelke, 1994, 1996; Wang, Hermer, & Spelke, 1999), as did human adults engaged in an attention-demanding verbal interference task (Hermer-Vazquez, Spelke, & Katsnelson, 1999). Both children and verbally distracted adults located an object after disorientation by searching in the correct relation to the shape of the room (a rectangle or a square with a bulge in one wall), but not by searching in the correct relation to a non-geometric landmark (a wall of a distinctive color and brightness or a distinct, familiar object). Rats' and humans' use of the shape of the layout to reorient or to navigate while disoriented provides evidence that some information about environmental shape was preserved over disorientation. Experiments 6 and 7 tested the hypothesis that disoriented observers retain accurate information about room geometry using exactly the same research paradigm as Experiments 1–5.

Experiments 6 and 7 were undertaken for a further reason: to address an alternative interpretation of the findings of Experiments 1–5. It is possible that the impairment to the spatial representations of object locations observed in those studies is an artifact of using the disorientation paradigm. The disorientation procedure used in the preceding experiments may have caused spatial representations to degrade for unknown reasons not addressed so far. If such an effect occurs, then spatial representations of environment geometry also should be impaired when subjects are tested using exactly the same procedure, measurements and analysis in the preceding experiments. In contrast, if representations of surface geometry are enduring whereas representations of objects are transient and egocentric, then only the latter should be impaired by disorientation.

7. Experiment 6

In this experiment, subjects were presented with a rectangular room furnished with four distinct objects arranged in a similar, but smaller, rectangular configuration. Each subject participated in an objects task and a corners task, in which they pointed to targets (objects or corners) without vision, both before and after disorientation. For each task, we obtained three error measures from subjects' pointing responses as before: the *heading error*, the *pointing error*, and the *configuration error*. If subjects form enduring representations of corners, then disorientation should produce an increase in heading error but no increase in configuration error. If subjects form transient, egocentric representations of corners as of objects, then disorientation should produce an increase both in heading error and in configuration error, above and beyond any increase predicted from the increase in pointing error.

7.1. Method

The experiment was conducted in a 1.8×2.6 m rectangular chamber with red fabric covering one short wall, in which four objects were placed adjacent to the walls so that they formed the same angular configuration as the four corners of the room (see Fig. 8).

Eight Cornell undergraduate students participated in two pointing tasks – one with objects and one with corners – separated by a short break. The order of these two tasks was counterbalanced across subjects. The procedure for the objects task was the same as for Experiment 2, except for the number and location of the objects. Objects were named once in a clockwise order and once in a counterclockwise order, starting randomly from one object. The corners task was identical to the objects task, except as follows. Instead of naming each target individually, only the first corner was named, along with the direction of the pointing sequence (e.g. 'start with the corner at the door and continue in a clockwise sequence'). Subjects proceeded with the four pointing responses at their own pace, and then they were asked to point again starting with the same corner and proceeding in the opposite direction. The data were coded and analyzed as in the previous experiments.

7.2. Results

In the oriented conditions of both the objects and the corners tasks, subjects maintained their sense of orientation, as indicated by their low heading errors

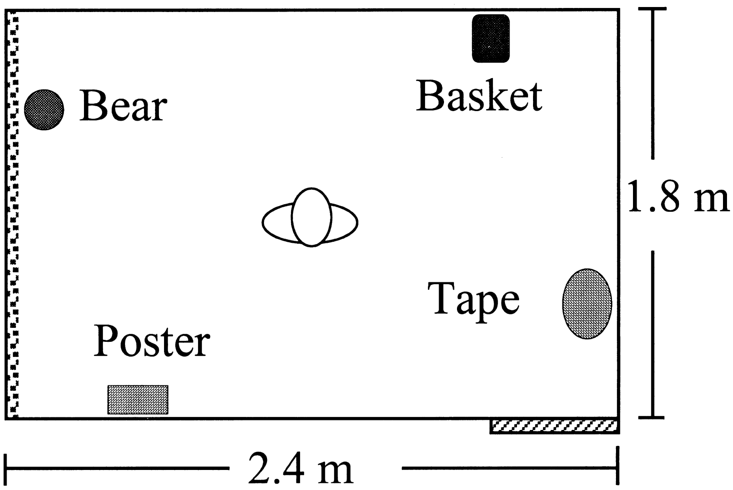

Fig. 8. An overhead view of the rectangular room for Experiment 6.

($\chi^2 > 29$, $P < 0.0001$). In the disoriented conditions of the two tasks, subjects were effectively disoriented, as indicated by their large and random heading errors ($\chi^2 < 5.5$, $P > 0.36$; see Fig. 9). Pointing error significantly increased after disorientation for the objects task (paired $t(7) = 2.9$, $P = 0.02$), but not for the corners task (paired $t(7) = 1.3$, $P = 0.24$). Turning to the most important analysis, subjects showed a significant increase in configuration error in the disoriented condition of the objects task, relative to the preceding oriented condition (paired $t(7) = 4.1$, $P < 0.005$), even after correcting for the pointing errors (paired $t(6) = 4.0$, $P < 0.01$).[7] In the corners task, in contrast, configuration error was not significantly different before and after disorientation (paired $t(7) = 0.2$, $P = 0.87$; see the left panel of Fig. 10). A 2 (task: objects versus corners) × 2 (condition: oriented versus disoriented) analysis of variance on the configuration error measure revealed a significant interaction between these factors ($F(1, 14) = 5.2$, $P = 0.04$). Configuration error was equally low in the two conditions of the corners task and in the oriented condition of the objects task, and it was reliably higher in the disoriented condition of the objects task.

7.3. Discussion

As in Experiments 1, 2 and 5, subjects who were disoriented pointed to multiple objects not only with a large heading error, reflecting errors in their assessment of their own orientation, but also with an increased configuration error, reflecting errors in their representation of object–object relationships. This finding therefore replicates the preceding experiments, despite changes in the placement of the objects (inside rather than outside the test chamber), the number of objects tested (four rather than six), the configuration of the objects (symmetric rather than irregular), and the order of retrieval (sequential rather than random). In contrast to these findings, subjects who were disoriented pointed to multiple corners of the room with a large heading error but low configuration error. Although the large heading error provides evidence that the subjects were disoriented in the corners task, as they were in the objects task, the low configuration error provides evidence that their representation of the shape of the layout survived this disorientation. These findings suggest that the overall shape of the layout is encoded as an enduring representation that is unaffected by disorientation. Moreover, the findings provide evidence that the impairment of the object representations after disorientation is not any artifact of the experimental procedure, measurement, or analysis, because it was not observed in the corners task despite the use of the same method. Thus, Experiment 6 provides further evidence that the spatial locations of objects are encoded in an egocentric reference frame and are individually updated over motions of the observer.

Before accepting these conclusions, however, we must consider whether stimulus or procedural differences between the objects and corners tasks account for the different findings obtained in those conditions. First, one may ask whether the

[7] Because one subject appeared to change his heading estimation between the two pointing sequences, therefore violating the assumption for this analysis, that subject was excluded from this analysis.

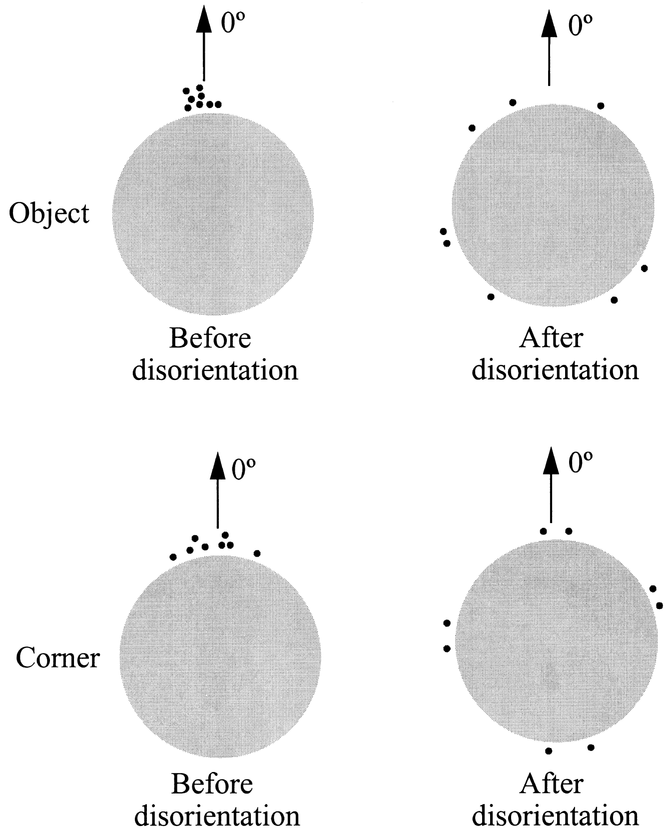

Fig. 9. The heading error in the oriented and disorientated conditions in Experiment 6. Each dot represents the heading error of one subject.

increase in configuration error stems from the fact that the targets in the objects task are closer to the subjects than are the targets in the corners task. Because any given spatial displacement causes a larger egocentric displacement for a nearby object than for a more distant object, one might propose that subjects encode all target positions allocentrically, that different object and corner positions are shifted, on average, to the same (allocentric) extent after disorientation, and that this shift produces a greater change in pointing to the objects because they are closer. The findings of Experiments 1, 2 and 5 provide evidence against this possibility, because the subjects in those studies pointed to objects that were outside the test chamber and considerably farther away than the objects or corners in Experiment 6. We conclude, therefore, that differences in the egocentric distances of the objects and corners fail to account for the difference in configuration error observed when pointing to objects versus corners.

A second difference between the objects and the corners tasks concerns the spatial properties of the targets. Corners project one-dimensional images in the visual

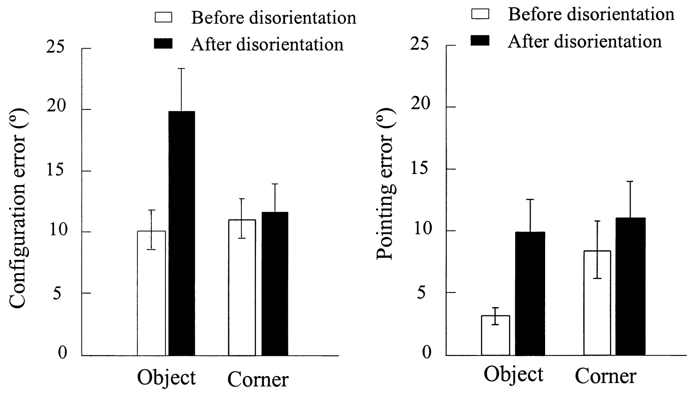

Fig. 10. The configuration error and pointing error in Experiment 6. The left panel shows the configuration error and the right panel shows the pointing error. The error bars are standard errors.

scene: they have vertical but no horizontal extent. As a result, a subject who points accurately to a corner will always point to the same horizontal position. In contrast, objects project two-dimensional images in the visual scene, with horizontal as well as vertical extent. Thus, a subject can point accurately to an object by aiming to different horizontal locations (e.g. its center versus its right border). This difference raises the possibility that disorientation brought about an inconsistency in subjects' choice of where to aim in pointing to an object, rather than an increase in configuration error. The analysis of configuration error in relation to pointing error nevertheless provides evidence against this possibility. If the increase in configuration error were due to changes in horizontal aiming for an object, then a comparable increase in pointing error should have been observed. Because the increase in pointing errors cannot account for the increase in configuration errors in the objects condition, we conclude that differences in the spatial extent of objects versus corners do not account for the differences in configuration error.

Although differences in target distance and pointing variability cannot account for the differences in configuration error observed after disorientation in the objects versus corners tasks, three further differences between these tasks indeed may have contributed to the differences in subjects' performance. First, our use of a highly salient, symmetric configuration may have increased the robustness of the representation of the room corners. Although the objects were arranged in the same rectangular configuration, the symmetry of this array may have been easier to detect and remember for corners than for objects, both because the corners are geometrically more simple and because they form a single, connected whole: the room. Detection of the symmetry of the room may have enhanced subjects' memory for the corner relationships and guided subjects' pointing to corners throughout the experiment, e.g. by inducing a strategy of separating all alternating points by 180°, thus reducing configuration error in the corners task. Second, subjects may have been more sensitive to the configuration of the four corners than to the configuration of the four objects, because the four corners were identical (except in color), whereas the four objects differed in shape, size, coloring, and function. Third, the procedure of naming each object individually during the pointing test but naming only one corner and a direction of motion (clockwise or counterclockwise) may have encouraged subjects to attend to the target configuration in the corners task more than in the objects task. The last experiment was undertaken to test all these possibilities against the alternative hypothesis that objects and room corners are encoded in different kinds of representations.

8. Experiment 7

Experiment 7 compared subjects' pointing to room corners with their pointing to objects both before and after disorientation. In this experiment, however, we used an irregularly shaped room instead of the rectangular room, and four identical objects instead of distinctive ones. In both conditions, subjects were given the same verbal commands, to point clockwise or counterclockwise to all targets (objects or corners), starting from a single verbally specified target. If the differing effects of disorientation on memory for the configuration of objects versus corners observed in Experiment 6 stemmed from the use of a salient symmetrical room of identical corners but different objects or of differing verbal instructions in the objects versus corners tasks, then this difference should disappear in Experiment 7. On the other hand, if the difference reflects the use of an egocentric updating process for objects and an enduring representation for corners, then the same pattern should be observed as in Experiment 6: disorientation should produce high configuration error in pointing to objects but low configuration error in pointing to corners.

8.1. Method

The experiment was conducted in a large, irregularly shaped room furnished with tables, a couch, cabinets, a sink and counter, and other objects. Four small, identical chairs were arranged in a smaller but similar configuration as the corners of the room, in a different orientation (see Fig. 11). Eight MIT undergraduate students pointed to the objects in one test and to the room corners in another test, in an order that was counterbalanced across subjects. No objects or corners were named during the pointing tests; instead, the subjects were asked to start with one object or corner (e.g. the one that was farthest away from them) and to point to all objects or corners in a clockwise or counterclockwise order. The procedure was otherwise the same as in Experiment 6.

8.2. Results

In both the objects and the corners tasks, subjects showed low heading errors in the oriented conditions ($\chi^2 > 38$, $P < 0.0001$) and high, random heading errors in the disoriented conditions, indicating that they were effectively disoriented ($\chi^2 < 2.4$, $P > 0.66$; see Fig. 12). Pointing errors did not increase significantly after disorientation in either the objects or the corners task (paired $t(7) < 1.6$,

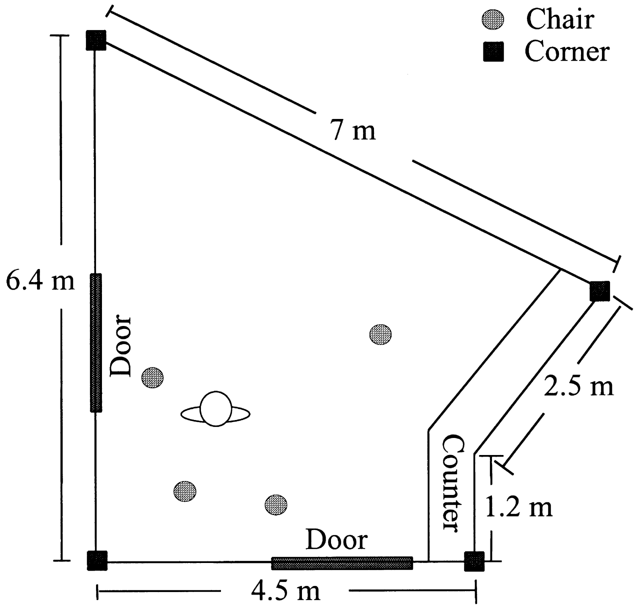

Fig. 11. An overhead view of the irregular room for Experiment 7.

$P > 0.16$; see the right panel of Fig. 13). The configuration error significantly increased after disorientation when subjects pointed to objects (paired $t(7) = 3.3$, $P = 0.01$), even after correcting for the pointing errors ($t(7) = 4.5$, $P = 0.003$), but it did not increase significantly when subjects pointed to corners (paired $t(7) = 1.5$, $P = 0.18$). There was a significant interaction ($F(1, 14) = 7.6$, $P = 0.02$; see the left panel of Fig. 13).

8.3. Discussion

The findings of Experiment 7 replicated closely those of Experiment 6. As in that experiment, disorientation had equal effects on the accuracy of subjects' perception of their own heading when they pointed to corners versus objects, but differential effects on subjects' representation of the relationships among the targets to which they pointed. When subjects pointed to objects, disorientation led to an increase in configuration error, providing evidence that object locations were encoded in an egocentric reference frame and updated over self-motion. When subjects pointed to corners, in contrast, disorientation led to no increase in configuration error, providing evidence that representations of corner locations were enduring and persisted over disorientation. This difference in pointing to objects versus corners was obtained even though the room was not symmetrical, the targets were homogeneous, and the instructions were identical in the two tasks. Even in an irregular room, therefore, the shape of the layout appears to be encoded independently of self-

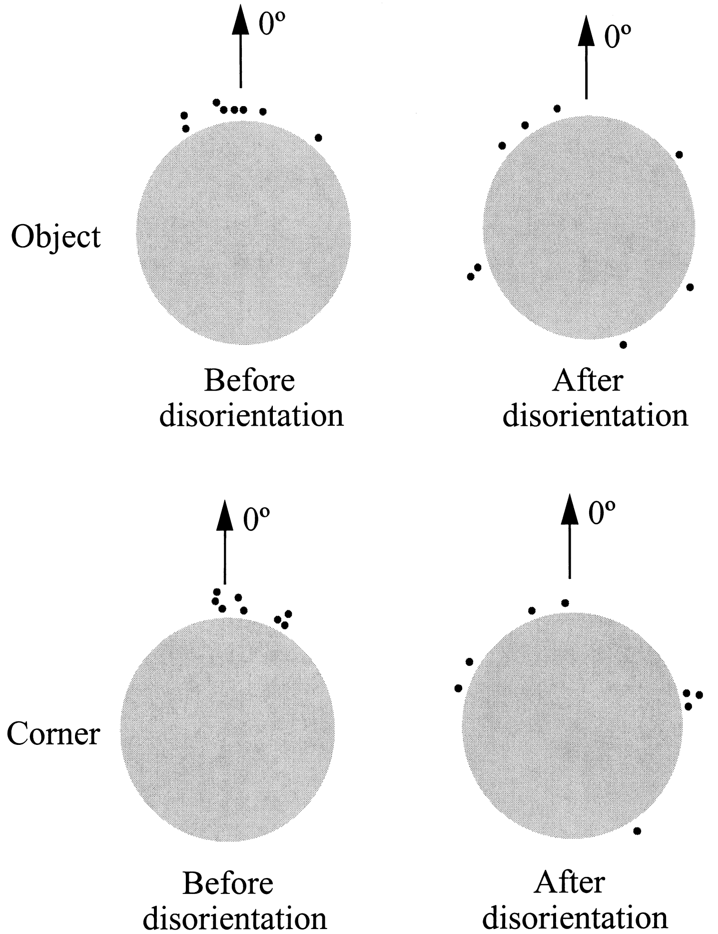

Fig. 12. The heading error in the oriented and disorientated conditions in Experiment 7. Each dot represents the heading error of one subject.

orientation. Moreover, even when objects are identical, their positions appear to be encoded in an egocentric reference frame and updated individually.

9. General discussion

The present experiments provide evidence that the representation of the relative directions of objects is impaired when subjects lose their sense of orientation. Subjects made significantly larger errors in their assessment of the spatial relationship among target objects, as measured by pointing to individual targets, after they lost track of their own orientation. This effect was not due to a decrease in pointing

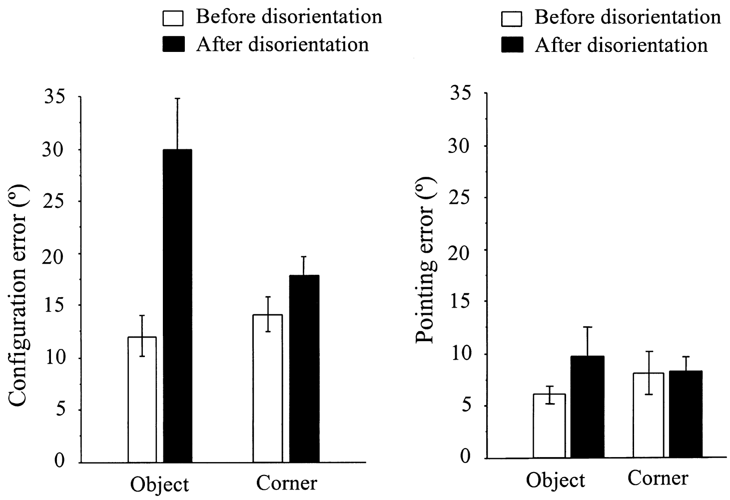

Fig. 13. The configuration error and pointing error in Experiment 7. The left panel shows the configuration error and the right panel shows the pointing error. The error bars are standard errors.

accuracy per se, was not a direct result of physical stimulation of the vestibular system, was not a consequence of changes or fluctuations in disoriented subjects' representation of their position or orientation, and did not result from general factors impairing memory such as the retention interval or the introduction of interpolated activity. The impairment was not reversed by reorientation using a single visual landmark, suggesting that the loss of accuracy of the representation is persistent. Using the same experimental procedure and measurements, we observed no effect of disorientation on representations of room geometry, suggesting that the phenomenon is not an artifact of the research paradigm and that it is specific to the representation of object locations. These findings shed light on the processes subserving human navigation and on their relation to navigation processes in other animals. Moreover, they place constraints on accounts of the representations that guide accurate navigation in humans, of the alternative spatial knowledge that humans resort to when their primary representations are perturbed by disorientation, and of the nature of the representations of environment geometry. We consider each set of implications in turn.

9.1. Spatial representations for navigation

The present findings suggest that human navigation in intermediate-sized, relatively novel environments depends on the active transformation of a representation of the positions of targets relative to the self: a representation that is updated as the navigator moves through the layout. This egocentric representation could take two forms. As in the McNaughton et al. (1995) account of rodent navigation, humans may maintain a representation of the current egocentric distances and allocentric directions of objects, as well as a representation of their own allocentric orientation, and they may update all these representations as they move. As an alternative possibility, humans may maintain purely egocentric representations of the distances and directions of objects, updating these representations as they move.

Either thesis would account for the phenomena observed in this study, because both are dynamic and transient in nature, such that the distance and direction of each target location relative to the self is specified directly and updated over locomotion. In both eyes-open and eyes-closed conditions of the present experiments, the subjects relied directly on the egocentric representations of the six non-visible targets to guide their pointing responses. Their estimation of the target locations remained reasonably accurate when they turned, with or without vision, as long as they were oriented and were able to update target positions continuously. After the breakdown of the updating process during the disorientation procedure, however, the subjects no longer had accurate representations of the egocentric directions of targets, which were the basis of the highly coherent pointing responses to different targets revealed in the conditions with intact orientation. As a result, they estimated target directions with less internal consistency. Although a single landmark served to reestablish subjects' global orientation, it did not serve to correct this configuration error.

These findings suggest that egocentric updating is the underlying mechanism for the path integration process, which is well known to be common to many animals from insects to humans (for discussion see Gallistel, 1990; Hermer & Spelke, 1996; Levinson, in press). In the simplest case, desert ants can represent the egocentric distance and direction of their nest and continuously update these values as they forage (Müller & Wehner, 1988). We propose that a 'cognitive map' is achieved by adding more environmental locations to the same processing system. Continuous updating of this egocentric map during locomotion could account for the classical demonstrations that a wide range of vertebrates move to familiar goals from novel positions and along novel paths. On this view, mammalian navigation is achieved through continuous enrichment of the core navigation system found in insects, rather than through the emergence of a qualitatively different, allocentric system (e.g. Gallistel, 1990; O'Keefe & Nadel, 1978; Tolman, 1948).

9.2. Object localization under disorientation

Although objects were localized less consistently when the subjects were disoriented, the configuration error was relatively small and localization was not by chance. In particular, most disoriented subjects pointed to objects in a pattern that preserved the objects' ordinal relationships. This finding indicates that some forms of spatial memory persist over disorientation. What might these spatial representations be? We discuss three possibilities.

First, disoriented subjects' above-chance consistency when pointing to multiple targets without vision could depend on a dynamic, egocentric spatial representation that persists over disorientation. Subjects may continue to update egocentric representations of target directions throughout the disorientation procedure of the present studies. The updated representations may become less coherent over the course of the disorientation procedure because of increased random errors in the disturbed updating process. However, the errors may be sufficiently small so as to preserve the ordinal relationships among targets.

As a second possibility, disoriented subjects may rely on a different egocentric representation: the remembered egocentric directions of objects prior to disorientation. Studies in cognitive psychology provide evidence that humans can form images of familiar but unseen environments. These images are egocentric, representing the environment from a particular point of view. The existence of egocentric images of the environment could account for disoriented subjects' above-chance consistency at pointing to different targets, whereas the lower accuracy of these images, relative to the dynamic egocentric representations that oriented subjects maintain and update over motion, could account for the decrement in pointing consistency caused by disorientation. One version of the egocentric image hypothesis was contradicted by our data. After disorientation subjects evidently did not point to the targets as if they were facing the same direction as in either the eyes-open or the eyes-closed condition, which is predicted by the hypothesis that they simply retrieved the image learned during previous conditions. Nevertheless, it is possible that subjects relied on a different egocentric image than the ones they experienced during the eyes-open and eyes-closed conditions.

As a third possibility, crude, allocentric knowledge may guide subjects' localization of targets (e.g. Huttenlocher, Hedges, & Duncan, 1991; McNamara, 1986; Stevens & Coupe, 1978). For example, the subjects in our experiments might have encoded the ordinal sequence of the target objects, which they then placed at equal intervals around themselves. Since the target objects were not evenly distributed around a circle, the variation of the six angles between adjacent objects should have decreased after disorientation. However, the data from Experiments 1 and 2 showed that the standard deviation of the six angles did not decrease after disorientation, as predicted by equal distance coding ($t(18) = -1.46$, NS), suggesting a richer representation of the target configuration. Further analyses tested various candidate representations without success.[8] It remains possible, nevertheless, that subjects used a different type of allocentric spatial representation to guide their pointing after disorientation.

[8] Further analyses of the angles between two adjacent targets tested whether the subjects maintained both a representation of objects' ordinal positions and a categorical representation of gap sizes between objects as 'large' or 'small'. If the big angles remain relatively big and the small ones small, there should be a strong correlation in the angular distances of adjacent targets between the conditions. There was no support for this kind of simple coding hypothesis. The average correlation between the eyes-closed condition and the eyes-open condition ($r = 0.88$) was significantly higher than that between the disorientation condition and the eyes-open condition ($r = 0.63$, $t(18) = 2.66$, $P < 0.016$). Of the 19 subjects tested with disorientation, only nine showed the two biggest 'gaps' in the right places after disorientation, in contrast to 15 in the eyes-closed condition. These findings suggest that the subjects did not rely on a sequential coding plus a categorical coding of gap size.

9.3. Representations of environmental geometry

Why do we form a representation of environmental shape that preserves its configuration over disorientation but a representation of object locations that does not? One possibility appeals to the purposes that spatial representations serve, in relation both to our evolutionary history and to our experience. The geometric structure of the surface layout generally persists much longer than the geometric relationships between distinct, movable objects (Gallistel, 1990), and so persisting representations of the layout may be more useful than persisting representations of object locations. In addition, objects tend to be the goals of our actions, and so egocentric representations of their positions may facilitate the guidance of action. A second possibility appeals to the perceptual organization of scenes. The movable objects in a room typically are perceived as an array of units that are relatively independent of one another. For example, three objects in a triangular configuration typically are perceived as three objects, not as one triangle. In contrast, a room may be perceived as a single unit, not as an array of separate walls and corners. Thus, the four right-angled corners of a room may be perceived as one rectangle, not as four corners, and so its parts may not be updated separately. Future experiments could test each of these possibilities. For example, it will be interesting to learn whether subjects show low configuration error for an array consisting of a single object, or for an array consisting of multiple, overlapping surface layouts. Experiments are planned to test these possibilities.

Whatever the reason for the difference we observe between spatial representations of objects and of the surface layout, that difference provides an explanation for the finding that animals and humans reorient themselves primarily in accordance with the geometry of the layout. In order for a disoriented navigator to reestablish his position and heading in the layout, the navigator must compare some visible features of his surroundings to a previous representation of the layout. In our experiments, representations of the shape of the surrounding layout were found to be stable and enduring over disorientation, whereas representations of movable objects were not. This difference could explain why animals and humans use information about the shape of the layout to guide their reorientation whenever such information is available. Ongoing research is investigating this hypothesis further by comparing in detail the cues used in a reorientation task (Hermer & Spelke, 1996) to those that survive a disorientation procedure.

In summary, when humans are tested in small-scale environments that are not highly familiar to them, their ability to accurately locate objects appears to depend on representations of the current egocentric distances and directions of objects, on a process that continuously updates those representations over locomotion, and on an enduring representation of environment geometry that may serve as a basis for reorienting (Cheng & Gallistel, 1984; Hermer & Spelke, 1996). Because humans create and use real allocentric, physical maps, it is perhaps surprising to discover that human spatial memory shows striking similarities with that of rodents and even insects. The present evidence nevertheless invites the view that all animals localize objects in qualitatively the same ways as do insects, by means of egocentric representations and updating processes. To be sure, mammals have more sophisticated visual systems than do insects, and so their representations of the egocentric locations of surrounding objects are richer than the ‘snapshot’ representations often attributed to bees and other insects (e.g. Collett, 1996). Mammals also have greater memory and processing capacity than insects, and so they can update simultaneously the egocentric locations of many more targets than does the foraging ant (e.g. Wehner & Srinivasan, 1981). Despite these quantitative differences, however, basic cognitive capacities may show the same broad continuity over phylogenesis as do other biological functions.

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