

Spatial Representations of Object Locations and Environment Shape

by

Ranxiao Wang

B. S., Genetics and Genetic Engineering
Fudan University, 1992

Submitted to the Department of Brain and Cognitive Sciences
in Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy in Computational Cognitive Science
at the
Massachusetts Institute of Technology

August, 1999

[September 1999]

© 1999 Massachusetts Institute of Technology.
All rights reserved.

MIT LIBRARIES
WITHDRAWN
FROM
JUL 20 2000
MIT LIBRARIES
SCHERING

Signature of Author: _____
Department of Brain and Cognitive Sciences
August 6, 1999

Certified by: _____
Elizabeth S. Spelke
Professor of Psychology
Thesis Supervisor

Accepted by: _____
Gerald E. Schneider
Professor of Neuroscience
Chairman, Committee for Graduate Students

MASSACHUSETTS INSTITUTE
OF TECHNOLOGY
WITHDRAWN
FROM
OCT 14 1999
MIT LIBRARIES
LIBRARIES

SCHERING PLOUGH

Spatial Representations of Object Locations and Environment Shape

by

Ranxiao Wang

Submitted to the Department of Brain and Cognitive Sciences
on August 6, 1999 in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy in Computational Cognitive Science

ABSTRACT

Previous studies show that rodents and human children can use the shape of the surroundings but not other non-geometric features to localize an object after disorientation, suggesting that different systems and mechanisms are involved in the representations of object locations and environment shape. This thesis reports three sets of studies investigating the nature of spatial representations and processes for navigation. The first set of studies provided evidence that children fail to use nongeometric information after disorientation even when geometric information is minimized and nongeometric information is highly familiar. The second set of studies suggest that human adults' representations of object locations are egocentric, updated over self movements. The third set of studies showed that unlike representations of object locations, environment shape is encoded directly and independent of self movements. These studies suggest that human and animals rely primarily on environment geometry for reorientation because of the invariant nature of these representations.

Thesis Supervisor: Elizabeth S. Spelke
Title: Professor of psychology

Acknowledgments

Few people go to Graduate School without any background in their chosen field. As one of them, life could not have been more difficult - for I knew practically nothing about psychology, or the brain, or cognition, or computer science, or linguistics - nothing but some vague eagerness to learn and do something interesting and intellectually challenging. So I owe my first thanks to Barbara Finlay, who generously admitted me into the Department of Psychology at Cornell, which completely changed the course of my life.

Thanks to Liz Spelke for having inspired my interests in cognition. Thanks to Tom Gilovich for telling me that people can do well and be happy only if they pursue their own interests. Thanks to my former advisor James Cutting for teaching me perception and for productive research on heading judgments. Thanks to the members of my advisory committee at Cornell - James, Liz, Tom, Bob Johnston and Dan Huttenlocher - for trust and complete freedom, and for the smiles when I claimed that I hated exams. Thanks to Linda Hermer as my first friend and collaborator, who taught me how to run experiments and what graduate life is like. And to Cornell - the most beautiful campus - which seems to be saying everyday that *learning is fun, research can be exciting, so enjoy graduate school!*

I am most grateful to Liz, who has always been so wonderfully enthusiastic, insightful and having hundreds of excellent ideas. Thanks to Steve Pinker, Nancy Kanwisher and Janellen Huttenlocher for serving as members of my thesis committee and for broadening and sharpening my thoughts. Thanks to Molly Potter for trust and support and wise suggestions on my job talk. Thanks to Ted Adelson and Hany Farid for teaching me computer vision. Thanks to Kara Ko and other graduate students for chatting and sharing ideas, to Kirsten Condry for help with equipment and settings, and to Denise Heintze for guiding me through the administrative maze.

I also thank Dan Simons, for being my collaborator and my non-official advisor. Moving to Boston at about the same time, I joined his friendly, brand-new lab and learned to overcome my shyness to speak out in a group.

Finally, my thanks go to the people in the Department of Psychology, University of Illinois at Urbana Champaign - David Irwin, Ed Shoben, Gordon Logan, Art Kramer, Chris Wickens, Karl Rosengren, Joe Malpeli and others - for a wonderful interview day, and for warmly inviting me to be a faculty member there.

This thesis is dedicated to my parents, to whom my happiness and well-being have been of central interests for the past three decades, and to my dear little brother who is not little any more - with love.

Table of Contents

I.	Introduction	5
II.	Chapter 1: Reorientation in Children	6
III.	Chapter 2: Egocentric Updating for Object Locations	27
IV.	Chapter 3: Invariant Representation for the Shape of the Environment	53
V.	References	73

Introduction

Navigation is an interesting phenomenon about which everyone has something to say. Some of us claim to be very poor at recognizing places and lose our sense of orientation after two or three turns, whereas other people claim to be expert navigators who are consistently oriented to their surroundings. Despite these differences, all normal people can remember many features of the environment, determine the directions and distances between environmental features, and decide how to get to known places from different starting points. What allows us to do so? What is the nature of the underlying representations and processes for place learning and navigation? Do humans have different types of representations and processes for different aspects of the environment and for different purposes? What is the evolution and the development course of spatial representations and strategies?

These questions require that researchers compare spatial representations and processes in animals, children and human adults in various tasks and paradigms. Using a disorientation paradigm, I have studied human children's and adults' representations of two aspects of the environment, the geometric shape of the layout and the locations of individual objects or features, investigating the reference frames for these representations, the dynamics in using these representations, and the different roles these representations play in navigation tasks. By comparing mechanisms of navigation revealed in children and adults with those previously found in animals, I hope to gain a better understanding of the fundamental structure of spatial knowledge across species.

This thesis is composed of three chapters, each addressing one component of the issue on the nature of spatial representations for navigation. Chapter one reports a series of studies investigating the restrictions in reorientation processes, which were first demonstrated in rodents (Cheng & Gallistel, 1984) and young children (Hermer & Spelke, 1994), to see whether children are able to use nongeometric information after disorientation when geometric information is minimized and when nongeometric information is highly familiar. Chapter two reports five experiments using a disorientation paradigm to investigate the nature of the spatial representations of object locations in human adults. Chapter three reports two studies further investigating whether representations of environment shape are different from those of object locations. Although the chapters are written to stand on their own, the studies are internally connected by the common research question, concerning what are the nature and roles of the spatial representations for various aspects of the environment. A version of Chapter one is in press in *Behavioral Neuroscience*. All references appear at the end of the thesis.

Chapter 1: Reorientation in Children ¹

Abstract

Neurophysiological studies show that the firing of place and head-direction [HD] cells in rats can become anchored to a variety of features of the perceptible environment, suggesting that those features partially specify the rat's position and heading. In contrast, behavioral studies suggest that disoriented rats and human children rely exclusively on the shape of their surroundings, ignoring much of the information to which place and HD cells respond. We explored this difference by investigating young children's ability to locate objects in a square chamber after disorientation. Children 18-24 months old used a distinctive geometric cue but not a distinctively colored wall to locate the object, even after they were familiarized with the colored wall over multiple sessions. Children's performance closely resembled that of rats, suggesting that the spatial representations underlying reorientation and object localization are common to humans and other mammals. Together with the neurophysiological findings, our experiments raise questions for the hypothesis that hippocampal place and HD cells serve as a general orientation device for target localization.

¹ A version of this chapter is in press in *Behavioral Neuroscience*. We thank James J. Knierim for comments on a draft of this paper and Kirsten Condry and Sarah Goldman for help in collecting data in Exp. 4. Supported in part by a grant to ESS from NIH (R37-HD 23103). Some of the findings were presented in poster format at the International Conference on Infancy Studies in Providence, RI, April 1996, and at the biennial meeting of the Society for Research in Child Development in Washington DC, April 1997. Address correspondence to Ranxiao Wang (francesw@s.psych.uiuc.edu).

The brain systems subserving navigation and spatial memory have been subjected to intense study at behavioral and neural levels, but two central questions remain unanswered. One question concerns the relation of spatial behavior to brain function. Studies of single neurons in actively moving rodents provide evidence that many neurons in the hippocampus are selective for an animal's position ("place cells") and that some neurons in the postsubiculum, thalamus, and striatum are selective for the animal's heading ("head-direction cells") (e.g., Dudchenko & Taube, 1997; O'Keefe & Nadel, 1978; O'Keefe & Speakman, 1987; Taube, Goodridge, Golob, Dudchenko, & Stackman, 1996; Taube, Muller & Ranck, 1990). Do these cells form a cognitive map by which animals locate themselves and significant objects within the environment, or are their location- and direction-specificity consequences of other functions? A second question concerns the relation of spatial memory systems in non-human mammals to those in humans. Humans in modern societies navigate quite differently from other mammals, using unique information sources (e.g., maps and verbal directions) to find their way in unfamiliar environments and ignoring other information sources (e.g., solar angle) used by a broad range of animals. Has the evolution of primates and humans brought fundamental changes to the systems subserving spatial memory and navigation, or do common mechanisms underlie these functions in all mammals?

Concerning the first question, neurophysiological studies indicate that rodent place and HD cells have specific receptive fields at certain spatial locations and directions, respectively. The activity of these cells persists when external sensory cues are removed, suggesting that the cells are selective for an animal's position rather than for any specific perceptible patterns (O'Keefe & Nadel, 1978). Moreover, disoriented animals sometimes show large and seemingly random rotations of the fields of place and HD cells, but the rotations of different neurons are correlated within a single animal, suggesting that these neurons form a unitary representation of the environment and of the animal's position and heading within it (Knierim, Kudrimoti & McNaughton, 1995). In experiments in richer environments with multiple cues, however, repositioning of individual cues affects some place cells but not others, suggesting limits to the unity of this representation (Gothard, Skaggs & McNaughton, 1996; O'Keefe & Speakman, 1987). Rodent place and HD cells clearly are involved in spatial memory and navigation, therefore, but their precise function is not known.

Concerning the second question, a series of behavioral studies of reorientation and spatial memory have yielded strikingly parallel findings in rats and human children aged 1.5 to 5 years. Cheng & Gallistel (1984; Cheng, 1986; Margules & Gallistel, 1988) and Hermer & Spelke (1994, 1996; Hermer, 1997) studied reorientation and spatial memory in participants placed in a rectangular chamber with multiple cues as potential landmarks. Participants were shown the location of a desired object (food for rats, a toy for children) that was subsequently hidden. Then

they were disoriented and were allowed to search for the hidden object. Rats and children searched with high and equal frequency at the location of the hidden object and at the geometrically equivalent location at the opposite side of the chamber. Their ability to confine their search to these locations indicates that they were sensitive to the shape of the enclosure and used this shape as a cue to target localization. Nevertheless, rats' and children's inability to choose the correct corner over the geometrically equivalent opposite corner suggests that their reorientation and target localization process is not sensitive to a wealth of nongeometric information, including the distinctive brightness or coloring of a wall (for children) or the distinctive texture, brightness and odor of a corner panel (for rats). The closely similar performance of rats and human children suggests that a common system underlies reorientation and object localization in rats and humans, and that this system computes the congruence between geometric representations of the perceived and remembered environmental layout.

There is a curious difference, however, between the findings of the above two sets of studies. Although disoriented rats and human children show striking insensitivity to nongeometric information in behavioral experiments, such information exerts a powerful influence on the firing patterns of place and HD cells in rats. If a rat explores an enclosed, cylindrical chamber with no landmarks except for one region of contrasting brightness (hereafter, a "cue card"), the activity of its place and HD cells typically becomes anchored to the card: When the card is rotated, for example, place and HD fields tend to rotate with it (e.g., Dudchenko, Goodridge & Taube, 1997; Goodridge & Taube, 1995; Knierim et al., 1995; Muller & Kubie, 1987; Taube et al., 1990). If place and HD cell activity signals the rat's perceived position and heading within the environment, then this rotation implies that the rat has reoriented itself in accord with a nongeometric cue. Behavioral and neurophysiological studies therefore suggest different conclusions about the nature of the reorientation and object localization process.

Two differences between the methods of the behavioral and neurophysiological experiments might account for their contrasting findings. First, behavioral studies of rats and children typically test participants in environments with a distinctive and informative shape, such as a rectangular chamber (Cheng, 1986; Hermer & Spelke, 1994) or a square chamber with geometrically distinctive internal landmarks (Biegler & Morris, 1993, 1996). In contrast, neurophysiological studies often situate rats in environments with minimal distinctive geometry: an enclosed cylindrical or square chamber devoid of geometric landmarks (Knierim, et al., 1995; Taube et al., 1990). Second, behavioral studies in humans have tested participants in novel environments, whereas neurophysiological studies typically have situated rats in familiar environments. Animals may use nongeometric cues only when geometric information is minimized and when the cues are familiar and stable. Consistent with the latter possibility, Knierim et al. (1995) found that place and HD cell rotations are more strongly anchored to a cue

card if an animal experienced the card at a constant location while it was oriented. When rats only experienced the card in a state of disorientation, the authors suggested, they had no opportunity to learn that the landmark occupied a stable environmental position (although see Dudchenko, Goodridge, Seiterle & Taube, 1997).

Three experiments investigated these possibilities by testing human children's object localization after disorientation under situations designed to approximate the situations faced by rats in neurophysiological studies. First, the task of Hermer & Spelke (1994, 1996) was given to young children in a square chamber with no distinctive markings (control condition), or with one distinctively colored wall (nongeometric cue condition). If the disorientation procedure was effective and no unintended directional signals were present in the environment, children were expected to search the four corners equally in the control condition. If the distinctive cue served as a basis for object localization after disorientation, then children were expected to search the correct corner with higher frequency in the condition where the cue was present.

Experiment 1

Children aged 18 to 24 months were tested individually in two unfamiliar environments: a square chamber with four white walls (control condition) and the same chamber with a shiny red fabric covering the wall opposite to the chamber's point of entry (nongeometric cue condition). In both conditions, a child watched a parent hide a toy in one corner of the chamber, was lifted and turned with eyes covered to induce disorientation, and then was released and encouraged to find the toy.

Method

Participants. Participants were 10 young children (six males and four females) aged 18 to 24 months (mean, 21.6 months), born of full-term pregnancies and suffering from no known health problems. Two of the children were eliminated from the sample because they failed to complete at least 3 valid test trials (see Coding & Data Analysis) in each experimental session.

Apparatus. The experiment took place within a 1.9m x 1.9m x 2.0m chamber situated in a larger experiment room (see Figure 1). The walls and ceiling of the chamber were covered with white, soft acrylic fabric stretched onto a concealed wooden frame. The chamber was accessed through a 0.7m x 2m door covered by the same white fabric. When the door was closed and the fabric was secured to the adjacent wall, the four walls looked identical to adults inside the chamber. The floor of the chamber was covered with a homogeneous gray carpet. At each corner of the chamber was a 1.1m tall red panel behind which a small toy could be hidden. Four 40W lights were positioned symmetrically on the ceiling to illuminate the chamber. A camera was mounted in the middle of the ceiling providing an overhead view of the chamber and sending the image to a

VCR outside the chamber. A radio also was positioned at the center of the ceiling to make soft constant noise which masked other sound sources.

In the nongeometric cue condition, a bright 1.9m x 2.0m red satin fabric was attached to the wall opposite the door. On entering the chamber, therefore, a child directly faced a smooth, shiny red wall flanked by matte, textured white walls. Informal observations of the children's behavior on entering the chamber suggested that the red wall was a salient feature of the environment (see Discussion below).

Design. Each child was given one oriented search trial followed by two test sessions, one in the white chamber and one in the chamber with the red wall. Each test session consisted of four disorientation trials in which the toy was hidden in the same corner as for the oriented search trial. The sex of the participants, the corner at which the target was hidden, and the order of the two test sessions were orthogonally counterbalanced across participants. The test sessions were designed so that the child would begin each of the four trials in a session facing the center of a different wall, but variations in parents' and children's behavior precluded our controlling the child's facing position exactly (see Coding & Data Analysis).

Procedure. The experiment was conducted by one experimenter outside the chamber and by one parent inside the chamber with the child. Detailed instructions about the procedures, but not the experimental hypotheses or previous findings, were given to the parent before the experiment. Then the parent brought the child into the chamber with a toy chosen from a collection outside the chamber. In each trial the parent showed the child the toy, played with it briefly, and then hid the toy behind a corner panel that was designated by the experimenter and shown to the parent before she went into the chamber. When the parent judged that the child had seen the hiding of the toy, he or she picked up the child and turned him or her one half to one full circle with eyes open (oriented search trial, presented first) or 4 full circles with eyes covered (disorientation trials). While the parent turned the child on disorientation trials, the experimenter walked around the outside of the chamber so as not to serve as a stable cue to orientation and then knocked on the center of a pre-chosen wall. The parent was instructed to put the child down at the center of the chamber facing the indicated wall and to encourage him/her to retrieve the toy while looking only at the child and not indicating any corner location by pointing or other means. The child might keep searching until s/he found the toy. If the child failed to retrieve the object after about 2 minutes of encouragement, the parent indicated the correct corner.

The child and parent left the chamber for a short break between the two test sessions, during which time the experimenter either introduced or removed the red wall. To maintain the child's interest throughout the experiment, breaks could be taken and the toy changed at any time, although the hiding location of the toy remained the same.

Coding and Data Analysis. An assistant who was naive to the experimental design and hypotheses coded the videotapes after the experiment was completed. First, for both the oriented search and disorientation trials, the coder determined the actual facing position of the child at the point where he/she was released; the facing position was coded as the wall or corner where the child appeared to be looking as soon as he/she stood stably. Second, the coder determined whether or not a trial was valid, excluding trials from the analysis if the parent pointed at one of the corners before the child overtly indicated a search, if the child refused to search for the object, or (for the disorientation trials) if the child was rotated less than 2 circles or with eyes open most of the time. Finally, the coder determined the location of the child's first search on each valid trial. The child was determined to have searched for the toy if he or she moved one of the panels, opened the bottom of the panel, or pointed at one of the corners and had the parent open it.

Results

Figure 2 presents the mean search rates at the four corners of the chamber for the two disorientation conditions. In the white chamber, the children searched randomly among the corners ($F(3, 21) = 0.43, p = 0.73$), indicating that the disorientation procedure was effective. The children still searched randomly with the red wall present ($F(3, 21) = 1.88, p = 0.16$). Children's search accuracy in the two test sessions did not differ ($t < 1$).

Further analyses investigated the effects of target corners, sex and order of sessions on the percentage of correct searches on the disorientation trials. The repeated sample ANOVA revealed no significant main effects or interactions involving the three factors (all $F_s < 3, p_s > 0.13$). Finally, we analyzed the relationship between the initial visibility of a corner at the start of a search trial and the child's tendency to search at that corner. If the child faced a wall after disorientation, the immediately visible corners were those adjacent to that wall; if the child initially faced a corner, that corner alone was counted as immediately visible. On average, 76% of searches in the red wall session and 74% of searches in the white chamber session were directed at an immediately visible corner ($t(7) = 3.0, p = 0.02$; $t(7) = 2.4, p < 0.05$, respectively).

A final analysis focused on children's performance on the oriented search trials. Of the 6 children with a valid oriented search trial, 5 (83%) correctly retrieved the toy (with chance = 25%, $t(5) = 3.5, p = 0.017$). Children did not confine their search to an immediately visible corner on the oriented search trials ($p = 0.68$).

Discussion

On the oriented search trials, children found the toy by searching directly the corner at which it was hidden. This finding indicates that the children understood the search task, were motivated to perform it, remembered the object's location, and acted successfully to retrieve the

object when in a state of orientation. On the disorientation trials in the white chamber, children searched the four corners randomly, providing evidence that they were disoriented and that no unintended cues from the parent or the chamber allowed them to reorient themselves or find the object. Most important, the children's search did not improve on the disorientation trials in the chamber with the red wall. Their random search suggests that they failed to use the red wall as a directional cue to locate the object after disorientation.

Children's failure to search the corner with the correct relation to the red wall was striking and surprising both to the parents and to the investigators, because children's behavior suggested that they were well aware of the red wall's existence. Many children touched the red fabric, pointed at it, said "red," or tried to remove it. These informal observations suggest that children may detect and remember information about a chamber but fail to use that information to locate objects after disorientation (Cheng, 1986; Hermer & Spelke, 1996).

The present findings cast doubt on one account of the difference between behavioral and neurophysiological studies of disorientation. The activity of place and HD cells in rats has been found to be linked to nongeometric cues under conditions that are very similar to those of the nongeometric cue condition of Experiment 1. In particular, rats tested in a gray square chamber with a white card covering one wall have shown rotations of the fields of their HD cells anchored to rotations of the white card (Taube et al., 1990), even though the geometry of the chamber was the same for the rats as for the children in Experiment 1, and it is unlikely that the salience of the white cue card was higher for the rats than was the salience of the red wall for the children.²

We turn next to the second account for the difference between behavioral and neurophysiological studies: Animals use nongeometric cues only when they learn that the cues occupy stable locations in the environment. A salient difference between the experimental paradigm of Hermer & Spelke (1996) and Experiment 1, on one hand, and the paradigms used in most neurophysiological studies, on the other, is that rats in neurophysiological experiments usually receive hours of familiarization training in the experimental chamber before they are tested in a state of disorientation, whereas children and rats in behavioral experiments often use tasks in novel surroundings.³ Though some experiments suggest that hippocampal neurons establish

² It might be suggested that the contrasting findings of Taube et al (1990) and the present experiment stem from the use of a brightness cue in their experiment (walls that were gray vs. white) vs. a color cue in the present study (walls that were white vs. red). This possibility cannot account for the discrepancy between behavioral and neurophysiological studies, however, because the behavioral studies by Cheng (1986) and Biegler & Morris (1993) used a brightness cue even more extreme than that of Taube et al (1990) (walls that were white vs. black) and found no evidence for use of the cue. Because rats are colorblind, it obviously makes no sense to use color cues in that species. Because human children are sensitive to color and attentive to it, the color contrast used in this experiment should have enhanced the salience of the nongeometric cue.

³ In the behavioral studies of Margules & Gallistel (1988), oriented rats were given extensive training in the test environment with nongeometric cues occupying fixed locations relative to the test box. Because the test box was rotated relative to the global environment, however, this training did not indicate that the cues occupied stable positions.

place fields rapidly in novel environments (Wilson & McNaughton, 1993), it is not clear whether nongeometric cues are encoded during that period. The next experiments therefore investigated whether children would learn to use a nongeometric cue (again, a single red wall in a square chamber) when given sustained exposure to it.

In a preliminary study, we attempted to train one child to use a nongeometric cue by giving him repeated experience with a disorientation test in the square chamber with one red wall. Instead of searching for a hidden object in a fixed corner of the chamber, the disoriented child was asked to find the door of the chamber so that he could go out to find a new toy. This child showed correct search on 2 of the 10 disorientation trials, performance not differing significantly from chance ($t(9)=0.38$, $p=0.71$). Moreover, there was no correlation between success and trial order ($r=0.44$, $p=0.19$), suggesting no learning effect over the trials. It is possible, however, that 10 trials in one visit were not sufficient for learning. Moreover, the disorientation procedure may have led the child to perceive the red wall as unstable, impairing the child's learning to use it as a directional cue. Indeed, the findings of Knierim et al. (1995; although see Dudchenko et al., 1997a) suggest that a nongeometric cue to orientation is more effective if the animal experiences it in a constant location over an extended period of time while in a state of orientation. Accordingly, Experiments 2 and 3 investigated whether children would use a nongeometric cue (the red wall) when that cue was both familiar and stable.

Experiment 2

Children were given a single free play session in a square chamber with one red wall. During this session, they remained oriented and moved between the chamber and the larger environment repeatedly. Then children watched the hiding of an object in the chamber, were disoriented, and were encouraged to find the object.

Method

Participants were two male and two female children aged 18 to 24 months (mean, 20.8 months), selected from the same population as in Experiments 1. The experiment took place within the same apparatus as the nongeometric cue condition of Experiment 1. Each child first participated in a half-hour free play session during which he or she was introduced into the test chamber with a parent and was encouraged to play with toys inside the chamber. Every 5-7 minutes, the experimenter opened the door and led the child out of the chamber for a short break to refresh his or her sense of orientation relative to the outside environment. During the break, the child selected new toys to bring into the chamber. Throughout the familiarization session, music was played from a fixed location outside the chamber to provide an additional directional cue.

After the familiarization session, the music was turned off and the child was given 4 disorientation trials, following the same procedures as in Experiments 1.

Results

Figure 3 presents the findings of this experiment. The children searched the correct corner of the chamber on 27% of the disorientation trials, performance not differing from chance ($t < 1$). All four children searched randomly among the four corners (Chi squares < 5 , $ps > 0.25$).

Discussion

After a single play session in which children repeatedly entered and departed from the test environment, children still failed to use a nongeometric feature of that environment to guide their search for a hidden object. This finding suggests that children fail to use nongeometric information even in familiar environments, but that suggestion must be qualified in two ways. First, it is possible that one half-hour session with 5 visits to the chamber is not sufficient for learning that the red wall occupied a stable location. Second, the play session with toys, designed to resemble rats' scavenging session with food pellets in the experiments of Taube et al. (1990) and Knierim et al. (1995), might have drawn children's attention away from the red wall.

To test further the effect of familiarization of the red wall on object localization, we conducted a final experiment in which four children were familiarized with the chamber over multiple sessions, and in which they played games designed to focus attention on the chamber and its nongeometric landmarks. One game, in particular, drew the children's attention to the fixed location of a hidden object seen from multiple perspectives, and served as a basis for testing children's object localization after disorientation.

Experiment 3

Four children participated in a study in the square chamber with one red wall. The children made multiple visits to the laboratory during a three-week period, accumulating 2.5 hours of familiarization with the environment. During these sessions, the children searched for hidden objects and played games with the red wall while remaining oriented to the environment. During two final visits, the children received the disorientation test trials of Experiment 1 with the red wall present. If children learn to use a nongeometric cue when it is familiar and stable, then they should have been able to find the toy on these test trials.

Method

Participants were three female children and one male child, aged 19.0 months to 25.2 months (mean, 22.4 months) at the beginning of the study. The children had no reported medical

problems and had never participated in any related research. The apparatus was the same square chamber with one red wall as in Experiments 1 and 2.

The procedure was explained to the children's mothers in detail, but the mothers were not informed about the research design or hypotheses until the experiment was completed. During the familiarization period, each child was given a series of oriented search trials similar to those of Experiment 1. A variety of toys were introduced to the mother and child, and the mother hid a succession of different toys at a single test corner, picked up the child, knocked at the red wall to draw the child's attention to it, and then turned the child up to 2 circles without covering his/her eyes. Then the child was put down in the center of the chamber facing a wall indicated by the experimenter, and s/he was encouraged to find the toy. These trials were interspersed with other games designed to enhance the child's interest in the environment, including a ball game played in the chamber, and a naming game in which the mother knocked at the red wall and encouraged the child to say "red". At no time during these familiarization sessions was the child turned with eyes closed or otherwise disoriented. Breaks were taken about every 10 minutes, during which the child left the chamber and chose new toys for the hiding game.

After the familiarization procedure, each child was given the standard disorientation trials of Experiments 1 & 2. In addition, three of the four children were given a new test of the child's ability to learn a direct response to the red wall in a disorientation condition: a new "music wall" game. The experimenter put a xylophone behind the red wall outside of the chamber and asked the mother to knock at the red wall. While she knocked, the experimenter played notes on the xylophone. Then the mother lifted the child, covered her eyes and rotated her for at least four circles to disorient her. After the child was put down facing a wall indicated by the experimenter, the mother asked her "where's the music?" If the child tapped the red wall and only the red wall, the xylophone music again was presented.

The first child (female) visited the lab three times during the first week and twice during a second week, with a one-week pause between the two blocks of visits due to a family vacation. During the first 3 visits the child and parent played games in the room, and the child received a total of 16 valid oriented search trials. In all, the familiarization sessions lasted a total of 155 min. The fourth visit consisted of 4 music game trials, followed by 7 disorientation trials. Finally, the fifth visit consisted of 6 disorientation trials.

The second child (male) had four familiarization sessions including a total of 16 oriented search trials, followed by two test sessions including 3 disorientation trials (session 5), and 5 disorientation trials (session 6). The third and fourth children (both female) had 3 familiarization sessions that included a total of 10 oriented search trials, a fourth session that consisted of 2 oriented search trials followed by 6-8 disorientation trials, and a fifth session that consisted of 5-6 music game trials.

The videotaped records of all sessions were reviewed by an assistant blind to the experimental hypotheses. The assistant determined the child's facing position, eliminated invalid trials, and determined the position of the child's first search on every oriented search, music, and disorientation trial, following the criteria for Experiment 1.

Results

The principal results for this experiment appear in Figure 4. For the oriented search trials, each child successfully retrieved the toy (mean accuracy 85%, $t_s > 5$, $p_s < .004$). For the disorientation trials, in contrast, none of the children retrieved the toy with above chance accuracy (mean accuracy 23%, $t_s < .68$, $p_s > .51$). All children searched among the four corners randomly (Chi squares < 3.3 , $p_s > .34$). All three children who were given the music game trials successfully tapped on the correct (red) wall (mean accuracy 94%, $p_s < .017$). Overall, search accuracy on both the oriented search trials and the music trials was significantly higher than on the disoriented trials (oriented search paired $t(3)=5.8$, $p=.01$; music paired $t(2)=6.08$, $p=.026$).

For the two children who received disorientation trials on 2 successive visits, a further analysis compared changes in search performance over the two test sessions. For the girl, performance dropped nonsignificantly from 43% to 17% ($t(11)=0.98$, $p=0.35$); For the boy, performance increased nonsignificantly from 0% to 60% ($t(6) = 1.8$, $p=0.12$); No significant changes occurred across both children ($F(1,16)=1.30$, $P=0.33$).

Discussion

Experiment 3 provided no evidence that familiarization with a stable nongeometric landmark allows children to use the landmark to reorient or relocate objects. In this experiment, the children spent two hours running around and playing in the square chamber with one bright red wall. During that time, they watched their mother knocking on the red wall dozens of times, and they were encouraged to talk about the red wall. Moreover, three of the children learned to play a game in which they were disoriented and then immediately turned to the red wall and knocked on it to make music. Despite all this experience with the room and its nongeometric landmark, the children never learned to use the red wall to locate the hidden toy.

In contrast, the children successfully found the toy when they were tested in a state of orientation. This finding, combined with findings in previous research (Hermer & Spelke, 1996) suggests that their failure with the red wall does not stem from limits on memory of toy locations, motivation to search for the toy, ability to notice, remember, and respond to the red wall itself, or ability to understand and perform the task. Rather, the failure seems to reflect an inability to use a nongeometric cue to relocate objects after disorientation.

The findings of Experiments 2 and 3 contrast with those of Knierim et al (1995) & Dudchenko et al. (1997a) by showing no learning effect on children's performance in an environment with a stable, salient nongeometric cue. Although different results might be obtained in an experiment with a longer period of familiarization with nongeometric landmarks, or in an experiment with older children who have a more mature hippocampus, these findings suggest that degree of familiarity of the test environment does not account for the difference between behavioral and neurophysiological studies of disorientation and object search.

General Discussion

In the present studies, disoriented children aged 18-24 months failed to use a distinctively colored wall to locate an object in a square chamber, even after they were familiarized with the chamber over multiple sessions. In contrast, oriented children located the object successfully. These findings provide further evidence that disoriented children, like rats, failed to use nongeometric information to locate objects (Cheng, 1986; Hermer & Spelke, 1994, 1996).

The present results could be explained in two different ways. One explanation proposes that children followed a *reorientation strategy* for locating the object: After disorientation, they first reestablished their sense of orientation and then localized the object whose position had been encoded in the same framework. The other explanation proposes that children followed an *associative learning strategy* for locating the object: They directly encoded and retrieved the spatial relationship between the hidden object and one or more features of the chamber. We discuss each potential explanation in turn.

Cheng and Gallistel were the first to propose that disoriented rats use a reorientation strategy to locate objects in a stable environment (Cheng, 1986; Margules & Gallistel, 1988). In their experiments, rats searched for food in the correct relationship to the shape of the room, but not in the correct relationship to the room's nongeometric properties, after only minutes of exposure to the room and the target. In other experiments, rats have been found to learn to locate objects in relation to nongeometric landmarks, but this ability either required weeks of training in which the landmarks and the goal move together from trial to trial (e.g., O'Keefe & Speakman, 1987; Dudchenko et al, 1997b), or showed incomplete learning, with rats learning to search for the goal near the landmark but not in a specific place relative to it (Biegler & Morris, 1993; 1996). In view of this contrast, Cheng and Gallistel proposed that rats preferentially locate objects by encoding their geocentric positions. When rats are disoriented, therefore, they locate objects by first reorienting themselves and then returning to the objects' geocentric positions. Specifically, reorientation depends on a process for aligning a representation of the remembered shape of the environment with its currently perceived shape, irrespective of its nongeometric properties.

Several predictions follow from the thesis that disoriented children use a reorientation strategy to locate objects in a stable environment. First, disoriented children should search for objects in correct relation to the shape of the environment and not in correct relation to nongeometric landmarks. These findings have been confirmed in numerous studies (Hermer & Spelke, 1994, 1996; Hermer, 1997; Hermer-Vazquez, 1997), including the present ones.

Second, children should use geometric cues to locate an object after minimal exposure to the chamber and the object, whereas they should only learn a relationship between a hidden object and a nongeometric landmark after extensive exposure. Experiments by Hermer & Spelke (1994, 1996) provide evidence that children learn to use geometric information after very brief exposure to the object and environment. In addition, research by Hermer-Vazquez (1997), testing children with a method similar to Biegler and Morris (1993, exp. 1) provides evidence that children fail to learn to locate a moveable hidden object in a constant relation to a moveable landmark over the course of one test session. Like rats (Biegler & Morris, 1993, 1996), the children learned that the target was near the landmark but not that it bore a specific spatial relationship to it.

A third prediction follows from the hypothesis that children use a reorientation strategy in our experiments: When a child is reoriented by a geometric cue, s/he should be able to localize all invisible environmental features in coherence, even if they are not specifically learned as targets. Hermer (1997) tested children 3-4 years old in the same reorientation task as in the current studies, except that the children learned two target locations in a rectangular chamber with a blue wall. When asked to indicate the two targets and the door of the chamber after disorientation without feedback, they indicated the correct locations and the geometrically equivalent, opposite locations with equal frequency, suggesting that they located each target in relation to the room geometry but not the wall color. More important, children's representations were coherent: if one target was localized 180° displaced from its true location, so was the other targets and the door. The simplest interpretation of these findings is that children used reorientation strategy to locate the hidden targets and reoriented by the shape but not the color of the environment.

Finally, the reorientation hypothesis predicts that disoriented children will rely on geometric information when searching for objects in a stable environment, but that oriented children will not rely on this same information when objects move. This prediction was tested and confirmed in three experiments by Hermer & Spelke (1996). In one study, for example, children watched a toy hidden in one of two distinctively colored and patterned boxes placed in two adjacent corners of a rectangular chamber with no other distinctive landmarks. Then the children's eyes were closed and the boxes were moved quietly across the chamber, so that the geometric and nongeometric properties of the hiding locations were dissociated (e.g., if a pink striped box previously appeared in a corner with a long wall on the left, that box now appeared in a corner with a long wall on the right). In one condition, children were disoriented while the boxes moved. In the other condition,

children remained oriented (with eyes closed) during this time. Children who were disoriented searched primarily at the corner box in the correct geometric configuration, ignoring that box's incorrect nongeometric properties. In contrast, children who were oriented first looked at the boxes' former positions (now visibly empty corners), then located the boxes on the other side of the chamber and searched the box with the correct nongeometric properties, ignoring its new geometric configuration. This double dissociation is striking, because children in the two conditions viewed exactly the same environment during encoding and test, and they were given the same search task. These findings provide clear evidence for a linkage between the use of geometric information and disorientation, in accord with the reorientation hypothesis.

The hypothesis that rats and children use a reorientation strategy faces two difficulties. First, it does not account for the findings of two very recent behavioral studies, focusing on learning to escape to a hidden platform (Dudchenko et al., 1997b; Martin, Harley, Smith, Hoyles & Hynes, 1997). In Dudchenko et al's studies, disoriented rats successfully located the platform in relation to a nongeometric landmark with little training, even though they failed to locate food in relation to a nongeometric cue when tested in a very similar environment. Dudchenko et al (1997b) proposed that rats reorient by nongeometric information in both foraging and escape tasks, but that the disorientation procedure to which they are subjected impairs either memory or motivation selectively, allowing the animals to use information about the location of a safe haven but not information about the location of food. If that interpretation is correct and applies to humans, then it supports the associative learning hypothesis, to be discussed below, and casts doubt on the view that children's search errors in the present studies stem from limits on their ability to reorient by nongeometric cues.

The second difficulty faced by the reorientation hypothesis comes from the findings of neurophysiological studies of place and HD cell activity. As discussed before, the place and HD cell system uses nongeometric information even when rats are disoriented, suggesting that the system has "reoriented itself" according to the nongeometric cues. Most dramatically, HD cell activity provides evidence for reorientation in accord with a nongeometric cue when rats are tested in the very same environment in which they fail to use this cue to guide their search behavior (Dudchenko et al, 1997a, b). As many investigators have noted, however, alternative interpretations of place and HD cell activity are possible. For example, these cells may capture richer information about the environment than animals typically use in order to reorient themselves and return to stable locations. Within the neurophysiological literature, numerous findings are consistent with this suggestion. For example, place cells have been found to show directional specificity in many environments (Gothard et al., 1996; O'Keefe & Burgess, 1996). Place cell activity also typically changes dramatically when an animal performs a new task in an unchanging environment (Wiener, Paul & Eichenbaum, 1989). Place and HD cell activity is affected by the

movements of behaviorally significant landmarks even when those movements occur in the animal's presence (Gothard et al, 1996; Taube et al, 1990; Taube & Burton, 1995). Because it is unlikely that a rat represents a change in its position when it changes direction, starts a new task, or views a moving pattern, these findings suggest that place and HD cells do more than record an animal's sense of its own position and heading. When a HD cell rotates with rotation of a nongeometric cue, therefore, it may be encoding a change in the environment rather than a change in the animal's sense of orientation.

We turn now to the alternative account of disoriented children's performance in object search tasks, whereby their search depends on an associative learning strategy. According to this account, both oriented and disoriented participants locate targets by drawing on knowledge of the spatial relationship between the target and relevant cues. If disoriented rats used this strategy, then the findings of the experiments of Cheng (1986), Biegler & Morris (1993), and others would imply that rats encode and use the relationship of a target to a geometric cue easily and readily, but encode and use the relationship of a target to a nongeometric cue only with difficulty. Those who accept this hypothesis are free to interpret the activity of place and HD cells as pure reflections of the animal's global sense of position and orientation. By this interpretation, animals compute their own sense of orientation according to a set of landmarks and reorient themselves accordingly when the landmarks move. Failure to locate a hidden object does not stem from a failure of reorientation, on this view, but from a failure of learning about or remembering the target's position in relation to those landmarks. This version of the associative learning hypothesis provides a natural explanation for the finding that rats' localization of objects is affected by task and motivational factors (Dudchenko et al, 1997b): when rats are disoriented in a foraging task or an escape task, they may use all the available cues in the chamber to reorient themselves (as suggested by their HD cell activity). Those cues may be associated with the escape platform more strongly than they are associated with the food location, however, and so they may guide the rat's behavior in an escape task but not in a foraging task.

The associative learning hypothesis can explain various findings from studies of children. Children use geometric cues but not nongeometric cues to locate an object after disorientation because they encoded the relationship of the object to the shape of the room but not its relationship to nongeometric landmarks. Children learned to use geometric cues immediately because they encoded that relationship readily. Moreover, children locate multiple targets coherently because they encoded the spatial relationships among the targets. Finally, children used the red wall to locate the music after disorientation because they encoded that relationship. When a target has a directly visible nongeometric feature (e.g., the red music wall in Experiment 3), children can find the target easily by searching for that feature.

Nevertheless, the hypothesis that children followed an associative learning strategy faces difficulties. First, in the current Experiments 1 & 3, children succeeded in finding the object when they were in a state of orientation. If the red wall allowed the children to reorient, then it is not at all clear why children should succeed at finding the object when oriented but fail when disoriented and reoriented. Second, if children can immediately encode and use the spatial relationship between two targets, the targets and the door (Hermer, 1997), it is not clear why they should fail in encoding and using the spatial relationship between a target and a colored wall.

Third, when children found the target in relation to the nongeometric feature, the coherence reported by Hermer (1997) for geometric reorientation did not occur. In Experiment 3, the first female participant looked for and acted on the red wall to make music but then failed to locate the hidden object in correct relation to the red wall or to the music on her first disorientation trial. The child's behavior on this trial was quite revealing. Immediately after disorientation, the child ran to the red wall, and banged it. When asked for the toy, she then searched in the opposite corner from the correct one. Therefore, even when this participant succeeded in using the red-wall-to-music relationship, she did not search coherently at multiple locations in relation to the nongeometric landmark. The lack of coherence between use of the red wall in the music task and in the disorientation task, which was replicated in the two other children who were given both tasks, calls into question any explanation of children's performance based on general limits to children's learning or memory.

Finally, the associative learning hypothesis fails to explain why children used one set of relationships (involving nongeometric cues) to find an object when they were oriented and a different set of relationships (involving the geometric configuration) to find the same object, in the same environment, when they were disoriented (Hermer & Spelke, 1996). These differences cannot be explained by task factors at the time of encoding or search, because the environments and search tasks were exactly the same for the oriented and disoriented children. Indeed, the methods and procedures of the two conditions were identical except for the presence or absence of disorientation.

These difficulties do not rule out the hypothesis that children used an associative learning strategy. As earlier debates over associative models of spatial memory have shown (cf Tolman, 1948), the associative learning hypothesis can always be amended so as to provide a post-hoc account of any findings. Simple versions of this account, however, do not appear to be compatible with the evidence from studies of children.

However one interprets the findings of behavioral studies of disorientation, these studies provide evidence for striking similarities between the performance of adult rats and young humans. The similarities suggest that reorientation and object localization depend on homologous mechanisms in the two species. Moreover, although the hippocampus is not fully mature in two-

year-old children, the similarities suggest that basic, mammalian mechanisms of navigation and spatial memory are present. If these suggestions are correct, then continued study of these systems across species and across development, using the widening array of tools of cognitive neuroscience, holds considerable promise for revealing these mechanisms and their interrelations.

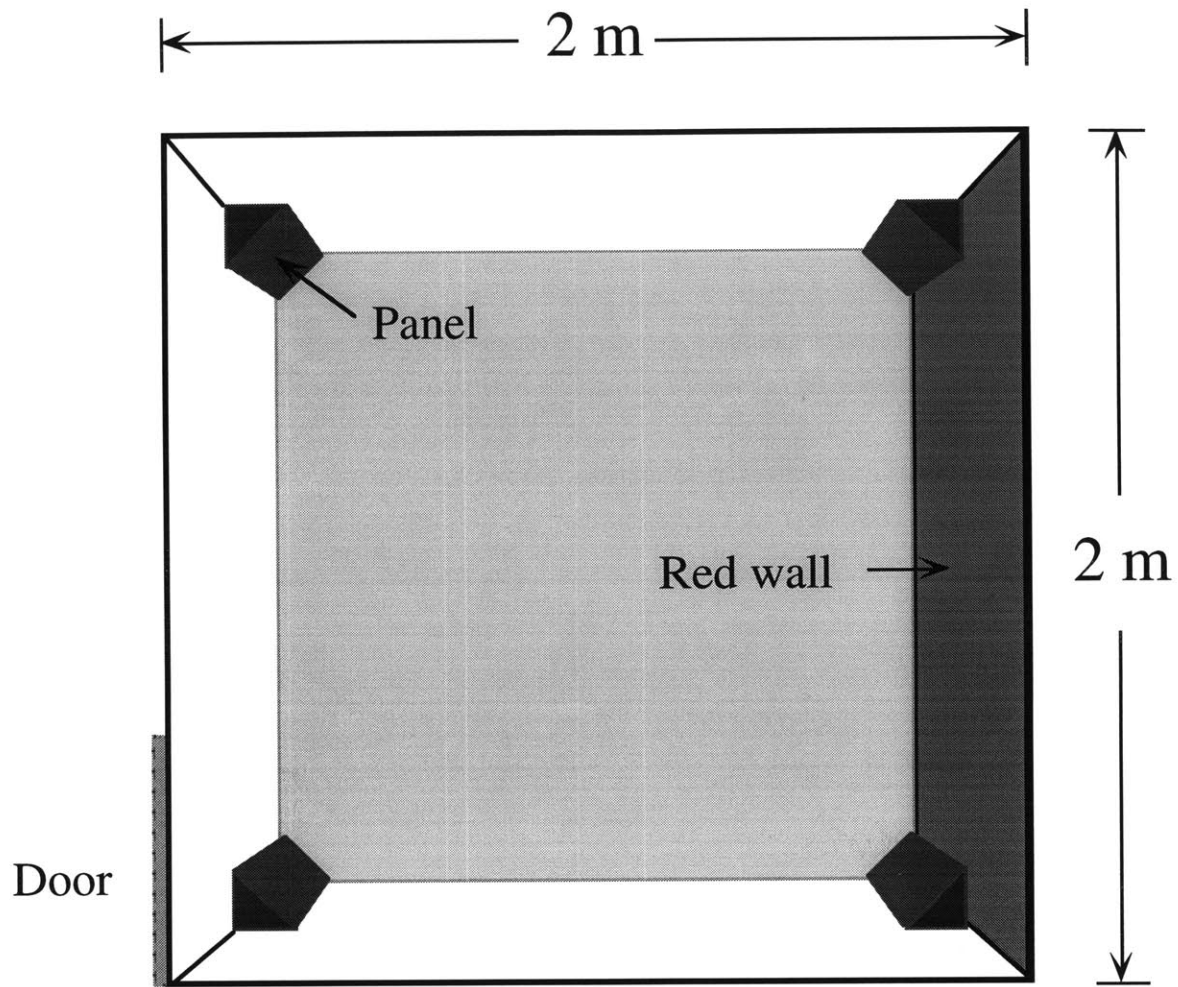


Figure 1: An overhead view of the square chamber with homogeneous gray floor, four identical white walls (one covered completely with a red fabric in one condition), four identical lights mounted on the ceiling (not shown), and one red panel at each corner behind which a small toy could be hidden. A video camera and a radio producing white noise were mounted at the center of the ceiling.

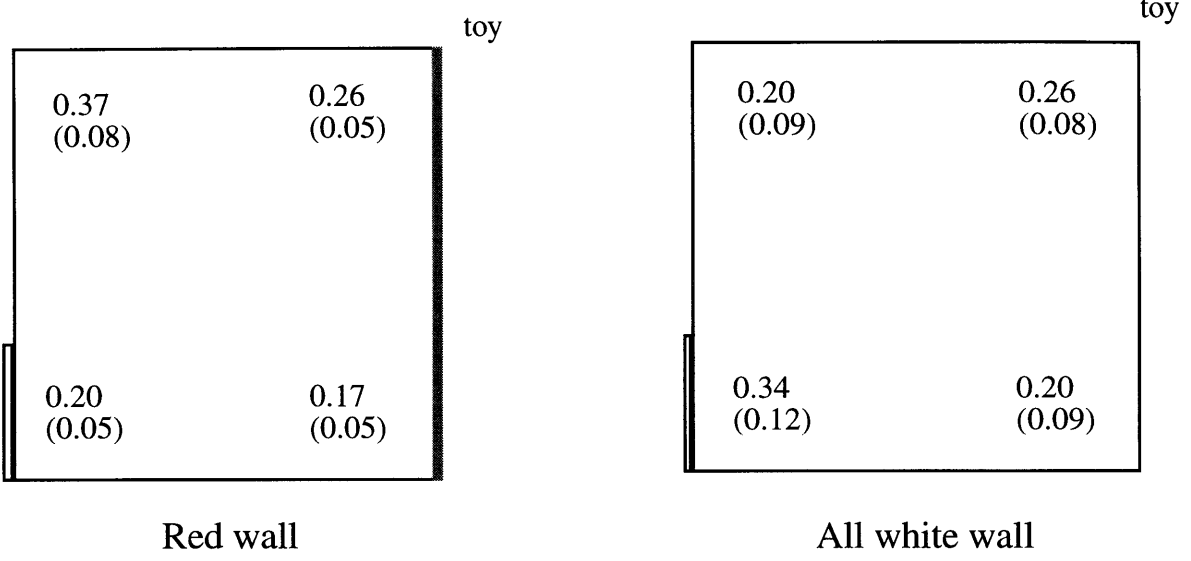


Figure 2: The mean proportion of search at each corner in the two disorientation conditions of Experiment 1. Standard errors are given in parentheses.

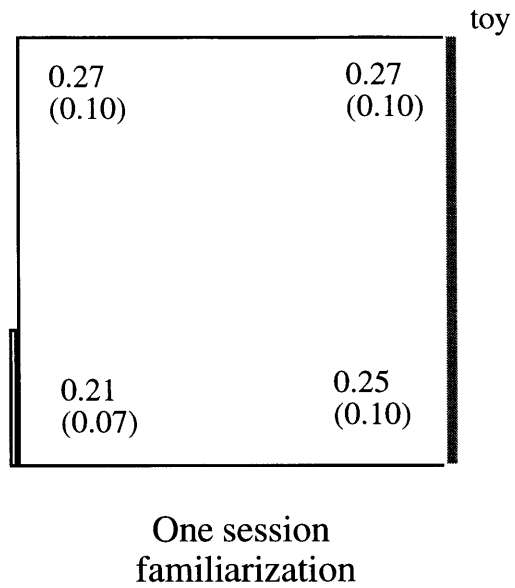


Figure 3: The mean proportion of search and standard errors at the four corners on the disorientation trials after the children had one free-play session in the chamber (Experiment 2).

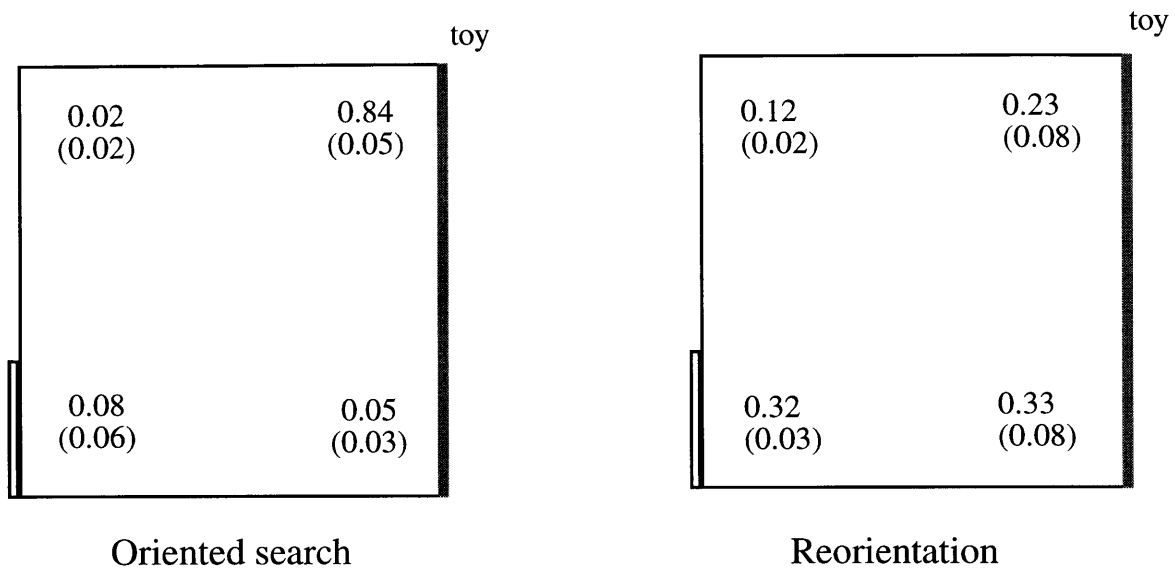


Figure 4: The mean proportion of search and standard errors at each corner in the familiarization sessions (oriented search trials) and the test sessions (reorientation trials) of Experiment 3.

Chapter 2: Egocentric Updating for Object Locations ⁴

Abstract

Five experiments tested whether human navigation depends on enduring, static representations of object-to-object relationships, or momentary representations of self-to-object relationships, updated over self-motion. Human participants 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 targets (“heading error”) but also the relative accuracy of pointing to different targets (“configuration error”), an effect not due to inaccuracy of the pointing response after self rotation, to the physical stimulation of the vestibular system, to an altered sense of position, or to any memory impairment caused by delays or interpolated activity. A single light providing a directional cue reduced both heading and configuration errors if it was present throughout the session. If the light was present during learning and test but absent during the disorientation procedure, however, participants 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 cast doubt on the view that accurate navigation depends on an enduring, static cognitive map. Like insects, humans appear to navigate most accurately by representing the egocentric distances and directions of objects and places and by continuously updating 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.

⁴ We thank James E. Cutting, Thomas D. Gilovich and Nancy Franklin for comments on earlier versions of this paper, and James Knierim, Linda Hermer, Richard Darlington, and William H. Warren for valuable discussions. Supported in part by a grant to ESS from NIH (R37-HD 23103). Exps. 2, 4 & 5 were presented at the 19th Meeting of the Cognitive Science Society, Stanford, CA (1997). Address correspondence to Ranxiao Wang (francesw@s.psych.uiuc.edu).

How do people and animals represent the spatial properties of their environment so as to locate objects and navigate effectively to significant places? Despite the large number of studies addressed to this question, the nature of mammalian spatial representations is still debated (Gallistel, 1990; McNaughton et al. 1995). Research on insects suggests that one form of navigation — homing — depends on egocentric representations of the environment, updated over self motion through a process of path integration (Srinivasan et al. 1996; Wehner and 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 et al, 1996; Mittelstaedt and Mittelstaedt, 1980; see Gallistel, 1990, for review). 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 and Nadel, 1978; Sutherland and Dyck, 1984; Tolman, 1948; see Gallistel, 1990 and Bennett, 1996, for discussion). Evidence for such cognitive maps gains much intuitive appeal from studies of humans. Although humans have a path integration mechanism that resembles that of insects and rodents (e.g., Berthoz et al. 1995; Fukusima et al. 1997), 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 angular relationships among 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 et al. 1995; O'Keefe and 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 et al. 1996; O'Keefe and Speakman, 1987; Quirk et al. 1990; see McNaughton et al, 1995, for review). 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 et al. 1995; Muller and Kubie, 1987). These findings suggest that ensembles of hippocampal neurons serve as a cognitive map of the environment (O'Keefe and Nadel, 1978; Wilson and 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 and Burgess, 1996; O'Keefe and 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 an accurate 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 animal's displacement vector, which is represented in egocentric coordinates relative to its previous position, to the vectors specifying each object's previous egocentric position. Thus, allocentric object-to-object relationships are not explicitly represented, although they can be derived from egocentric representations.⁵ According to the 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 and McNamara, 1998; Roskos-Ewoldsen et al. 1998; Shelton and McNamara, 1997; Sholl, 1987; Tarr, 1995; Tarr and Pinker, 1989; Tarr et al. 1997). Moreover, humans update these representations according to their own movements in order to recognize the scene or localize an object from a different viewpoint effortlessly (Farrell and Robertson, 1998; Fukusima et al. 1997; Simons and Wang, 1998; Wang and Simons, in press). The existence of these abilities nevertheless does not reveal whether human navigation depends primarily on egocentric updating or on an allocentric map.

⁵ 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).

The present research attempts to address this question through studies of human navigation. Our experiments depend on a central difference between an observer-free allocentric map 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 an allocentric map, which itself is independent of the position of the animal, then disorientation should disrupt the absolute accuracy, but not the internal consistency, of localization of multiple targets. Fully disoriented participants will not be able to aim with accuracy to any locations on the map: although participants will 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 participants have guessed their own position and heading, however, the directions in which they localize a set of objects should depend on the same stored representation of environmental locations that they use when oriented. Spatial localization by oriented and disoriented participants therefore should show equal internal consistency when tested under otherwise equivalent conditions: A disoriented participant's egocentric localization of all targets should deviate from that of an oriented participant by the same vector, equal to the difference between the participant's true vs. guessed allocentric orientation and position.⁶

Contrasting predictions come from the hypothesis that humans navigate most accurately by means of an egocentric representation, updated as they move, because such representations depend on the integrity of the updating process. Egocentric representations can be transformed accurately when one is able to continuously assess one's orientation and position. When one loses one's sense of orientation, however, this updating process is disrupted by definition. If the egocentric positions of different objects are represented and updated independently, then the internal consistency of pointing to different targets should be reduced by disorientation. A disoriented participant's pointing therefore should show not only an overall shift but also inconsistency among different targets.

Five experiments compared participants' pointing in the directions of a set of unseen targets when they were disoriented vs. oriented. To simplify the analysis of these experiments, the disorientation procedure focused on participants' representation of their heading direction: Participants turned inertially while maintaining a constant position within the chamber. We assumed that this procedure would lead participants to make random assessments of their heading, which in turn would produce a global shift in pointing to all targets. If participants pointed to the targets by means of an enduring, static cognitive map, then disorientation should not perturb the

⁶ In this paradigm a static egocentric representation (e.g., snapshots or viewer-centered representations) behaves in a similar manner as an allocentric map, therefore they can not be distinguished.

internal angular relationships among targets. In contrast, if participants pointed to the targets using egocentric representations computed by continuous updating, then disorientation should impair the updating process and produce an increase in configuration error.

Experiment 1

In this experiment, participants pointed to six targets first with their eyes open, then blindfolded after a small rotation, and finally blindfolded after disorientation. The initial eyes-open session provided a measure of the represented target locations by each participant. The first eyes-closed session served as a measure of pointing accuracy without vision in a state of orientation, after updating for a small rotation. The final disorientation session, in which the participants 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 participants were disoriented.

Method

Participants. Participants were ten Cornell undergraduate students, and recruited from psychology classes, who received course credit for their participation.

Apparatus. Testing took place within a 1.9m x 1.9m x 2.0m 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 6.15' x 6.45' red satin fabric was attached with Velcro to one of the four walls, which it then covered completely. The chamber was accessed through a 0.7m x 2m door in the wall opposite to the location of the red wall, as shown in Figure 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 40W 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 book shelf 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 during the intervals was carried by the experimenter moving about the chamber to eliminate any fixed auditory directional cues.

Procedure. Each participant was tested individually. The participant 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. Participants 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 participant 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, participants 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 2s (eyes-open session). Each participant pointed to each object four times, for a total of 24 pointing responses. Then the experimenter blindfolded the participants and turned them to face a different orientation randomly determined. The participants again pointed to the objects as announced (eyes-closed session). Then the participants were disoriented by turning around by him/herself for 1 minute without opening his/her eyes while standing in the chamber. Although some participants 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 participants 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 session).

The participants stood throughout each session and then changed facing orientation at the start of a new session. For each session and participant, facing direction was predetermined and pseudo-randomized among the 8 directions (four corners and four walls) so that each session has a different facing direction.⁷ The experimenter moved continuously inside the chamber throughout each session so as not to serve as a directional cue.

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 degree 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 session. This was taken as the *represented direction* of that target for that participant. The *individual error* was the mean difference between the pointing responses to each object in each of the following sessions and the *represented direction* of that object. This indicated how many degrees each object was "moved" from its original direction. The mean of the 6 individual errors in each session therefore measured the degree of displacement in the participant's assessment of his

⁷ 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 sessions, and the disoriented subjects faced a random orientation as a consequence of the procedure itself.

or her own heading (*heading error*), which should be small when the participants were oriented and be randomly distributed on the circle when they were disoriented. Whether the participants were disoriented or oriented during a given session was then tested using the Chi square test described by Batschelet (1981).⁸ 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 6 individual errors, which would be 0 if all 6 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 target in each session was calculated and averaged across 6 targets to compare the variability of repeated pointing responses to a single target (*pointing error*). Participants' ability to remember the ordinal relationship among the targets also was assessed by comparing the clockwise sequence of the 6 objects in the first eyes-open session with that in each of the subsequent sessions.

Results

Heading error. The upper panel of Figure 2 presents the errors in the represented facing directions for each participant during the eyes-closed and disorientation sessions. Although the facing directions represented by participants were quite accurate in the eyes-closed session (Chi square (5) = 50.0, $p < 0.0001$), those represented by participants after disorientation were random (Chi square (5) = 6.8, $p=0.24$). These findings indicate that participants' sense of orientation was preserved with eyes closed but was fully disrupted by the disorientation procedure.

Configuration error. The lower left panel of Figure 2 presents the internal consistency among the pointing responses to different objects in the two test sessions. The configuration error is significantly higher in the session that immediately followed disorientation than in the eyes-closed session ($t(9) = -2.39$, $p < 0.05$). All 10 participants gave the correct clockwise sequence of the 6 targets in both sessions.

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

⁸ 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 Chi square test, indicates a non-random distribution, which implies that subjects are oriented or mis-oriented systematically.

Discussion

The participants showed a significant decrease in the internal consistency among target locations after they were disoriented. This suggests 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, participants 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 observer-free 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, disorientation may leave participants' 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 participants' ability to point in the directions where they represented the targets. As a second example, the increase in configuration error might stem from disoriented participants' representation of a change in their position as well as their orientation. If participants pointed at targets from a new represented position, then the angular relations among targets should change, even if the cognitive map itself were unaffected. Second, participants' representations of the environment may be impaired, but not because of their loss of a sense of their own orientation *per se*. In particular, participants' 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.

To determine whether participants' inaccuracy in the disorientation session 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 participants 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 also were tested further in Experiments 4 and 5). Finally, in Experiments 4 and 5, we compared the configuration error of participants 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.

Experiment 2

In Experiment 2, participants participated in the same three sessions as in Experiment 1, with two changes in procedure. First, participants 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, participants 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, were caused by effects of the disorientation procedure on participants' 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.

Method

Participants were 10 Cornell summer school students who volunteered for the experiment. The participants sat in a swivel chair with rotatable seat that stood in a fixed location at the center of the chamber. For the disorientation procedure, participants turned while sitting in the chair by pushing against the floor with their feet for one minute. Participants pointed to each target twice in each of the three sessions, for a total of 12 pointing responses/ session. The method was otherwise the same as in Experiment 1.

Results

As shown in the top panel of Figure 3, participants showed little heading error with eyes closed, indicating that they maintained an accurate sense of orientation (Chi square (5) = 50.0, $p < 0.0001$). In contrast, participants showed large and random heading errors after the disorientation procedure, indicating that they were disoriented (Chi square (5) = 2.00, $p = 0.85$).

As shown in the lower left panel of Figure 3, the configuration error increased in the disorientation session, compared to the previous session in which participants pointed with eyes closed in a state of orientation ($t(9) = 2.65$, $p < 0.05$). Three of the 10 participants made at least one error on the ordinal sequence of the 6 targets in the disorientation session, whereas no participant made such an error in the eyes-closed session.

The lower right panel of Figure 3 presents the mean SD of the pointing responses to individual objects in the two test sessions. Pointing errors were significantly higher in the disorientation session than in the eyes-closed session ($t(9) = 2.43$, $p < 0.05$).

Relation of configuration error to pointing error. In both Experiments 1 and 2, participants 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. Since higher variability in the pointing responses will result in less accurate pointing to each target, this decrease in response accuracy could itself cause a decline in the internal consistency of pointing to different targets, even if pointing is guided by an enduring and accurate cognitive map. If variability in pointing was the sole cause of the increase of configuration error, the magnitude of the increase in configuration error will be predictable from the increase in pointing error. We tested this relationship, assuming homogenous variance of the pointing responses to all targets. 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

$$\text{Predicted configuration error} = \text{pointing error} / \text{sqrt}(N)$$

Since there was no significant difference in the disorientation sessions between the two samples ($t(18) = 0.98, p = 0.34$), we combined the data from Experiments 1 and 2, as shown in Figure 4. The observed increase in configuration error after disorientation was significantly higher than that predicted from the increase in pointing errors ($t(19) = 2.243, p = 0.034$). The internal consistency of localization of different targets therefore was reduced by disorientation, over and above the effect of disorientation on the consistency of localization of individual targets.

Discussion

The participants in Experiment 2 showed large heading errors after the disorientation procedure, indicating that rotating on a fixed chair was as effective at disorienting the participants as was standing and turning. Moreover, the participants showed a significant increase in configuration error in the disorientation session, 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 participants' 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.

The decrease in the consistency of pointing responses to different targets significantly exceeded what would be predicted, on statistical grounds, from the decrease in consistency of the different pointing responses to individual targets. This finding is important for two reasons. First, it shows that the effect of disorientation on configuration error is not a statistical artifact. Second, it shows that this effect does not stem from fluctuations, over the course of a pointing test session, in disoriented participants' representation of their own orientation. If configuration error were lowered after disorientation because disoriented participants experienced illusory changes in their

own orientation over the course of a test session, then this effect should have been just as strong when participants pointed to the same target at different times as when they pointed to different targets. The findings of Experiment 2 therefore cast doubt on the view that disorientation impairs a person's sense of direction but leaves intact an enduring, observer-free cognitive map.

Nevertheless, it may take longer than 30 seconds 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 pointing response after the same procedure in a task which required accurate motor control but no memory for the spatial directions of objects.

Experiment 3

In Experiment 3, participants 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 participants were oriented vs. disoriented. If the disorientation procedure directly affected participants' motor control but not their spatial memory, then the participants 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 participants' memory for the relationships among the target objects, then the participants in Experiment 3 should not show this impairment.

Method

Participants were 8 Cornell undergraduate students, recruited and compensated as in Experiment 1. Each participant pointed 4 times in each of six directions in each of three sessions (24 pointing responses/ session), 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 6 egocentric directions (front, back, right, left front, left back, right back) for this pointing task. To assure that the participants were disoriented, they were asked after the disorientation session 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.

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 participant 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 participants were effectively disoriented (Chi square (5) = 5.50, $p=0.36$), as shown in the top panel of Figure 5.

The lower left panel of Figure 5 presents the configuration error, again measuring the internal inconsistency of pointing in different directions, in the eyes-closed and the disorientation sessions. The participants showed a slight decrease in configuration error in the disorientation session, 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 sessions before and after disorientation ($t(7) = -0.61, p = 0.56$). As indicated in the lower right panel of Figure 5, the mean pointing error also showed no significant difference across the two sessions ($t(7)=0.11, p=0.92$).

Discussion

Participants 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 sessions, but it cannot account for the increase in configuration error observed in the disorientation sessions 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 participants engage in potentially interfering spatial activities, and it causes the participants 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 participants' loss of their sense of orientation, in contrast, then the increase in configuration error should not occur if the participants 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.

Experiment 4

In Experiment 4, participants were given the same pointing task for the same three sessions as in Experiment 3: 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, participants were tested with a blindfold that was translucent rather than opaque, through which a single asymmetrically placed light produced a detectable brightness gradient. Although participants could not see either the targets or any other features of the room, the brightness gradient allowed them to maintain a sense of 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.

Method

Participants were 10 Cornell summer school students who were recruited as in Experiment 2. Participants 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 participants 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 session, all testing took place with participants wearing a translucent blindfold. For the initial eyes-open session, participants 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 session). Finally, participants turned in the chair exactly as in Experiment 2. When they stopped, the experimenter again turned the participants to face about 20°-30° to the right or left side of the directional light and they pointed to the targets again (oriented rotation session). Half of the participants turned left in the eyes-closed session and right in the disorientation session, and others did the reverse. This manipulation facilitated participants' perception of the light through the blindfold.

Results

Figure 6 (top panel) presents the heading errors for each participant in the eyes-closed and rotation sessions of the experiment. Errors were small in both eyes-closed and oriented-rotation sessions, indicating that participants were well oriented in both sessions (respective Chi squares (5) = 50.0 and 29.6, $p < 0.0001$).

The lower left panel of Figure 6 presents the mean configuration error in each of the two test sessions. In contrast to Experiments 1 and 2, the configuration error decreased non-significantly in the session that followed self-rotation compared to the eyes-closed session ($t(9) = 0.99, p = 0.35$): 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 Figure 6, the pointing error also slightly decreased in the session after rotation ($t(9) = 1.08, p = 0.31$).

Discussion

Although participants received the same vestibular stimulation from the same self-rotation procedure as in the previous experiments, they showed only small heading errors after the procedure. This finding indicates that participants were able to use the light as a directional cue to maintain their sense of orientation. More important, participants' configuration error was as low in the test session that followed this procedure as in the test session 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 a decrease in the consistency of object localization, 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 participants' 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 participants' sense of orientation, in accord with the egocentric updating hypothesis.

Nevertheless, all the findings reported so far are consistent with the contrary hypothesis that human navigation depends on an enduring, observer free cognitive map that becomes temporarily inaccessible when the navigator is disoriented. It is possible that humans 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 participants are disoriented, therefore, their enduring cognitive map will not be accessible to guide their navigation.

The last experiment was undertaken to distinguish this hypothesis from the hypothesis that humans navigate by updating an egocentric representation, by investigating whether information about the correct relationships among objects is recoverable after a participant'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 participant's own position or motion, and so any impairment to this

representation due to disorientation must be transitory, caused by the temporary inaccessibility of the representation. If participants 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 be reversed.

Experiment 5

In Experiment 5, participants 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 session and then re-illuminated for that session. Therefore, participants 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 cognitive map that is accessible only when they are oriented, then the participants in Experiment 5 should have shown both accurate and consistent pointing after disorientation. In contrast, if humans navigate accurately by means of egocentric representations that are updated over motion, then the participants in Experiment 5 should have pointed with smaller heading errors than in Experiments 1 and 2 but with as large an configuration error as in those experiments. Although the reintroduction of the light should correct for the global error in participants' representation of their own orientation, it should not restore the dynamic, egocentric representation of target positions that was impaired during disorientation.

Method

Ten participants 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 participants began the disorientation procedure, and it was turned on again after the participants stopped turning. The final pointing test was given 30 s after the light was turned on. Thus, participants became disoriented during the turning procedure and were given time to reorient by the light before the last pointing test.

Results

The upper panel of Figure 7 presents the heading errors for each participant in the two test sessions of the experiment. Overall rotations were small in both the eyes-closed session and the reorientation session. In both sessions, participants showed an accurate sense of orientation, as in Experiment 4 (respective Chi squares (5) = 39.2 and 29.6, $p < 0.0001$).

The lower left panel of Figure 7 presents the configuration error in the two test sessions. Configuration error was significantly higher in the reorientation session than in the preceding eyes-

closed session ($t(9)=4.0, p < 0.005$). There was no significant difference in pointing error between the two sessions ($t(9)=1.4, p = 0.20$; see the lower right panel of Figure 7). In both sessions, all participants gave the correct clockwise ordering of the targets.

Comparing the reorientation session in Experiment 5 to the disorientation session 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 session in Experiment 5 than in the oriented rotation session in Experiment 4 ($t(18) = 3.5, p < 0.003$). There was no significant difference among the preceding eyes-closed sessions in the three experiments ($F(2, 27) = 2.0, p=0.15$).

Discussion

The single light introduced after the disorientation procedure of this experiment effectively corrected participants' heading error but not their configuration error. Although exposure to a single light source allowed participants to correct for their overall sense of orientation, this directional cue did not contain sufficient information to enable participants 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 target localization depends on an enduring static cognitive map that is made inaccessible by disorientation. Instead, people appear to rely on an egocentric map that is continuously updated from the previous one using estimations of ego motion. Such a representation appears to be irreversibly impaired by disorientation, which defeats the continuous updating process.

General Discussion

The present experiments provide evidence that the representation of the relative directions of objects is impaired when participants lose their sense of orientation. Participants made significantly more 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 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 participants' representation of their position, 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. These findings shed light both on the processes subserving human navigation and on their relation to navigation processes in other animals. Moreover, they place constraints on accounts both of the nature of the representations that guide

accurate navigation in humans and of the alternative spatial knowledge that humans resort to when their primary representations are perturbed by disorientation. We consider each set of implications in turn.

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 McNaughton et al. (1995)'s 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 by adding a vector of their own egocentric displacement relative to their current position.

Either thesis would account for the phenomena observed in this study, because either kind of egocentric spatial representation system operates as a path integration system, in which the distance and direction of each target location relative to the self is specified directly and updated over self motion. In both eyes-open and eyes-closed sessions of the present experiments, the participants would rely directly on the egocentric representations of the six non-visible targets to guide their pointing responses. Their estimation of the target locations would remain reasonably accurate when they turned, with or without vision, as long as they were oriented and allowed to update target positions continuously. After the breakdown of the updating process during the disorientation procedure, however, the participants 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 sessions with intact orientation. As a result, they estimated target directions with less internal consistency. Although a single landmark served to reestablish participants' global orientation, it did not serve to correct this configuration error.

The underlying mechanism for updating an egocentric map is akin to the path integration process, which is well known to be common to many animals from insects to humans (see Gallistel, 1990; Hermer and Spelke, 1996; Levinson, in press, for discussion). In the simplest case, desert ants have been found to represent the egocentric distance and direction of their nest and to continuously update these values as they forage (Muller and 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 and Nadel, 1978; Tolman, 1948).

Object localization under disorientation

Although objects were localized less consistently when the participants were disoriented, localization was not at chance. In particular, most disoriented participants 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?

Disoriented participants' above-chance consistency when pointing to multiple targets without vision could depend on an egocentric spatial representation that persists over disorientation. Participants 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 participants 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, presenting the environment from a particular point of view. The existence of egocentric images of the environment could account for disoriented participants' above-chance consistency at pointing to different targets, whereas the lower accuracy of these images, relative to the dynamic egocentric representations that oriented participants 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 participants 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 sessions, which is predicted by the hypothesis that they simply retrieved the image learned during previous sessions. Nevertheless, it is possible that participants relied on a different egocentric image than the ones they experienced during the eyes-open and eyes-closed sessions.

As a third possibility, crude, allocentric knowledge may guide participants' localization of targets. For example, the participants 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 two adjacent objects should have decreased after disorientation. However, the data from Experiments 1

and 2 showed that the standard deviation of the 6 angles did not increase after disorientation, as predicted by equal distance coding ($t(18) = 1.46$, n.s.), suggesting a richer representation of the target configuration. Further analyses tested various candidate representations without success.⁹ It remains possible, nevertheless, that participants used a different type of allocentric spatial representation to guide their pointing.

Although our studies provided evidence for updating egocentric representations, it is possible that humans form accurate static spatial representations when the environment is highly familiar and overlearned (such as the locations of furniture at one's home or office) or when the scale of the environment is larger (such as buildings on campus or in a city). Furthermore, the objects we tested were unrelated random objects. It is possible that humans form coherent spatial representations, whose internal consistency is preserved over disorientation, when in an environment whose diverse features are strongly related (e.g., the corners of a room or the parts of a unitary, spatially extended object). Ongoing studies are investigating these possibilities.

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, and on a process by which those representations are continuously updated over self motion. Although we cannot exclude the possibility that allocentric spatial representations exist in humans, they do not appear to account for humans' most acute sense of where things are.

Because we are the only species to create and use real allocentric, physical maps, humans are the species for which the cognitive map hypothesis is most plausible. The present evidence therefore invites the view that all animals navigate in qualitatively the same ways as do insects, by means of egocentric representations and path integration 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 use path integration processes to update simultaneously the egocentric locations of many more targets than does the foraging ant (e.g. Wehner and Srinivasan, 1981). Despite these quantitative differences, however, basic cognitive capacities may show the same broad continuity over phylogenesis as do other biological functions.

⁹ 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 sessions. There was no support for this kind of simple coding hypothesis either. The average correlation between eyes-closed session and eyes-open session ($r = 0.88$) was significantly higher than that between disorientation session and eyes-open session ($r = 0.63$; $t(18) = 2.66$, $p = 0.016$). Of the 19 subjects tested with disorientation, only 9 showed the two biggest "gaps" in the right places after disorientation, in contrast to 15 in the eyes-closed session. Therefore it does not seem like the subjects were relying on a sequential coding plus a categorical coding of gap size.

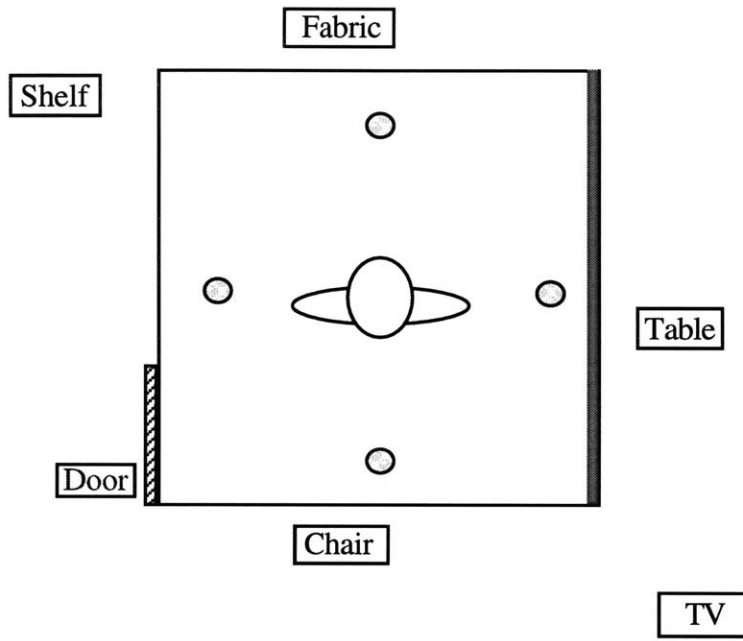


Figure 1. An overhead view of the experimental chamber.

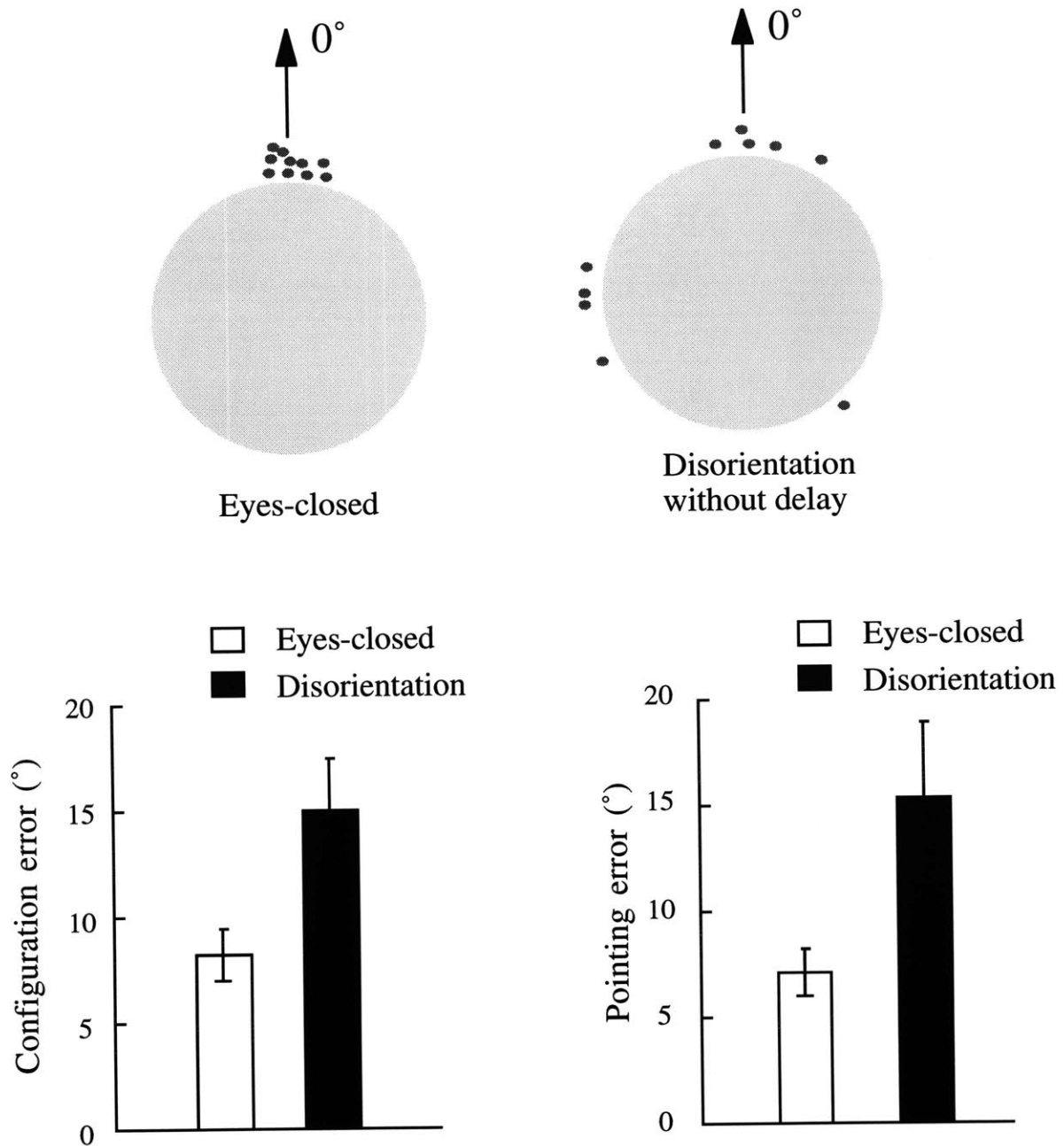


Figure 2. The heading error, configuration error and pointing error in Experiment 1. The top panels show the heading error in the eyes-closed and disorientation-without-delay sessions. Each dot represents the heading error of one participant. The lower left panel shows the configuration error and the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

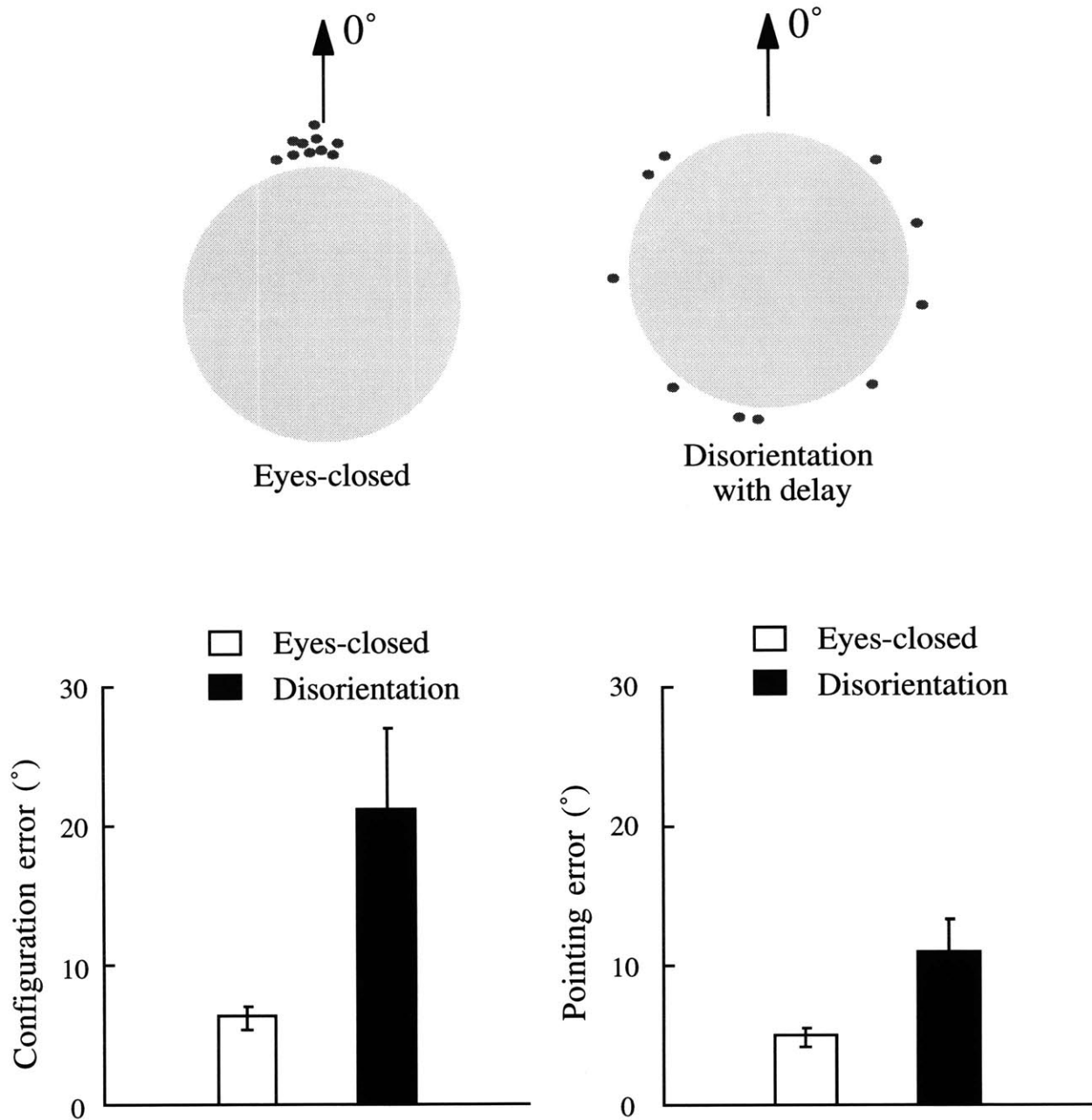


Figure 3. The heading error, configuration error and pointing error in Experiment 2. The top panels show the heading error in the eyes-closed and disorientation-with-delay sessions. Each dot represents the heading error of one participant. The lower left panel shows the configuration error and the lower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

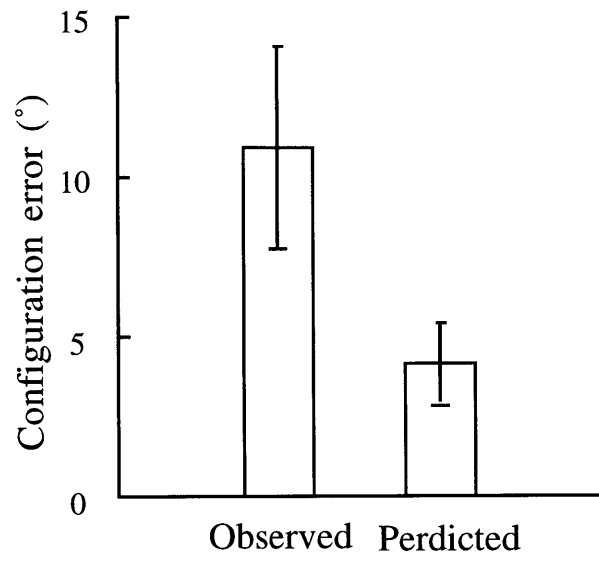


Figure 4. The observed configuration error and configuration error predicted from variation of pointing errors in Experiments 1 & 2.

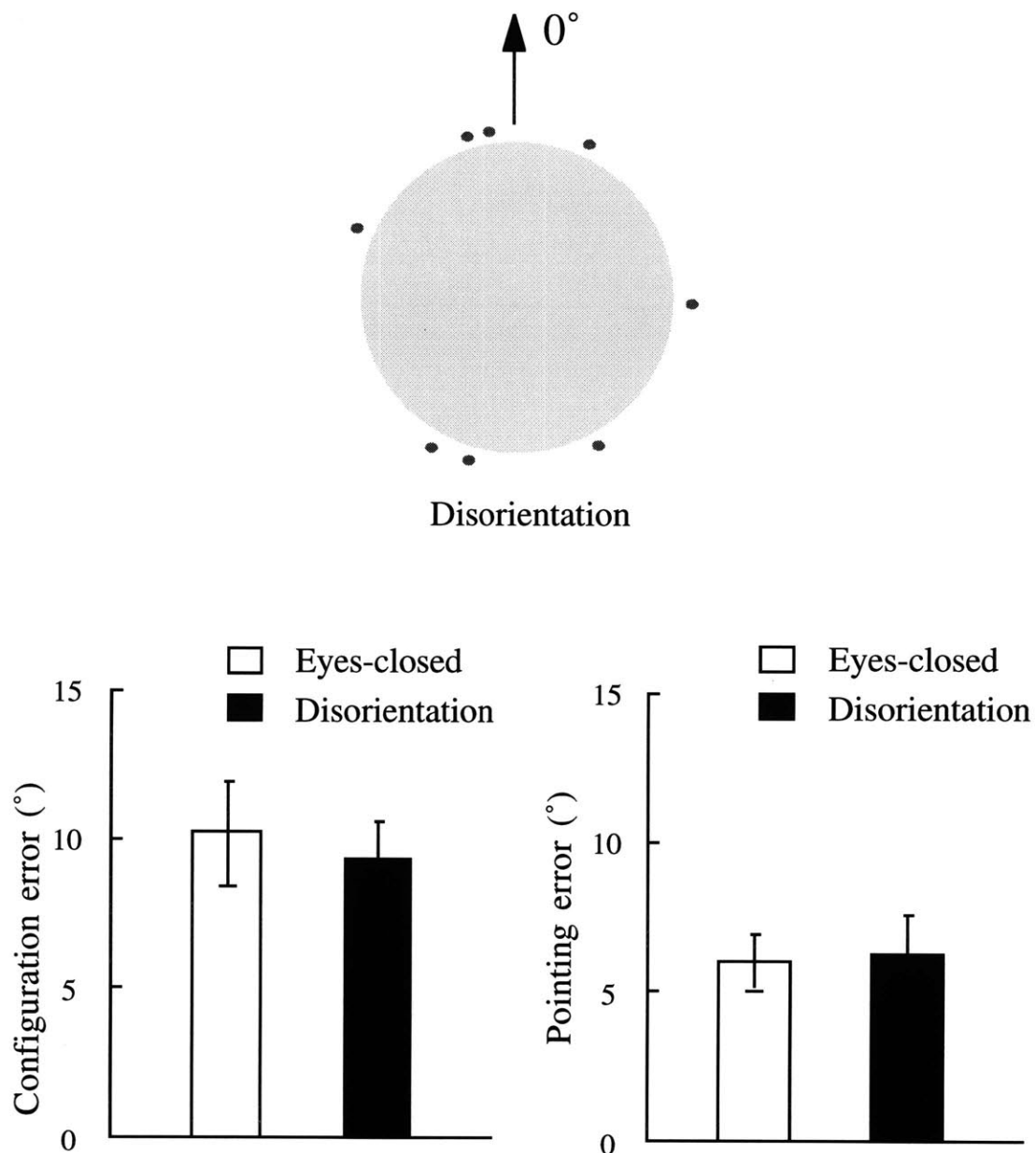


Figure 5. The heading error, configuration error and pointing error in Experiment 3. The top panel shows the heading error in the disorientation sessions. Each dot represents the heading error of one participant. The lower left panel shows the configuration error and the lower right panel shows the pointing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

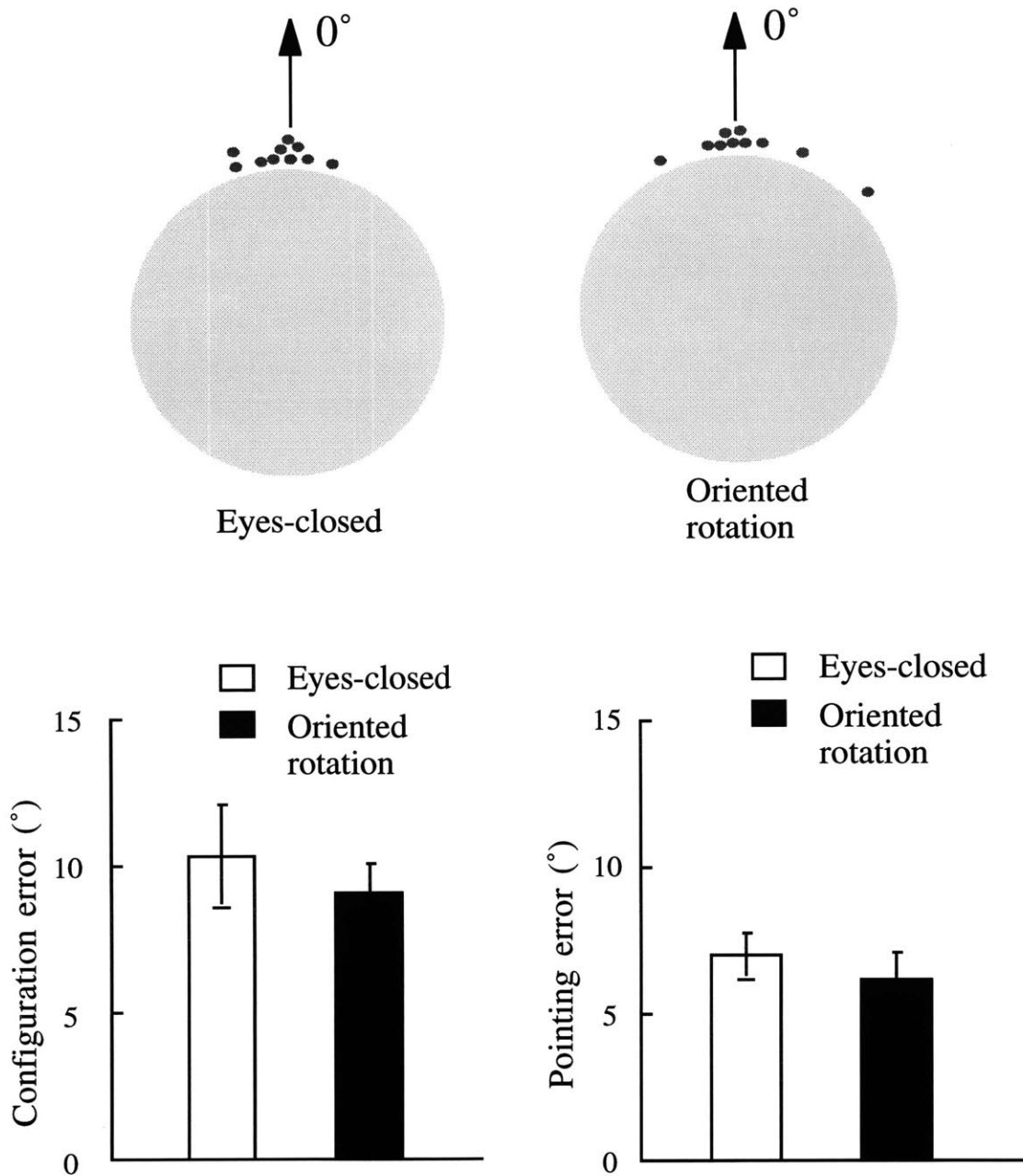


Figure 6. The heading error, configuration error and pointing error in Experiment 4. The top panels show the heading error in the eyes-closed and oriented-rotation sessions. Each dot represents the heading error of one participant. The lower left panel shows the configuration error and the lower right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

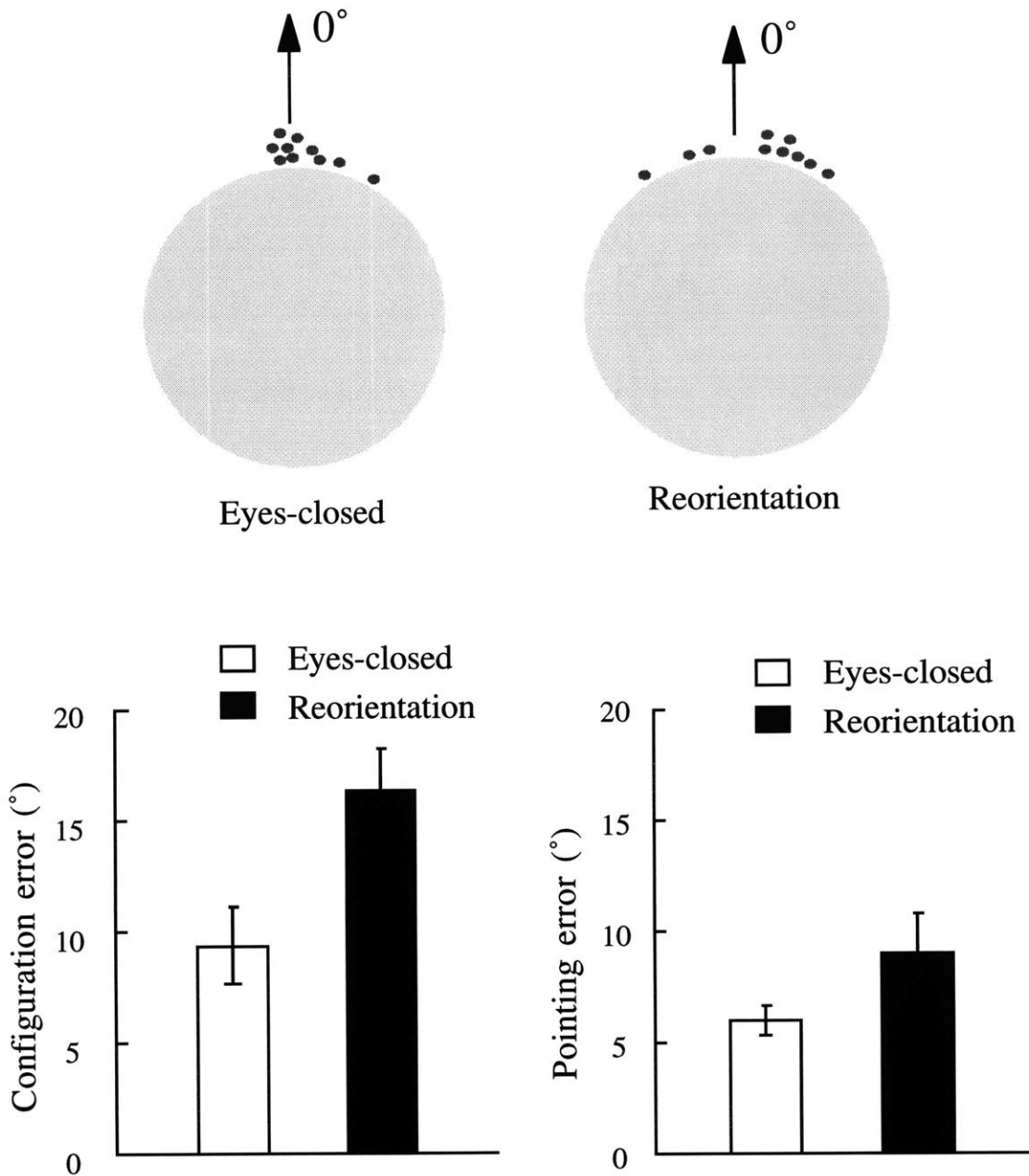


Figure 7. The heading error, configuration error and pointing error in Experiment 5. The top panels show the heading error in the eyes-closed and reorientation sessions. Each dot represents the heading error of one participant. The lower left panel shows the configuration error and the lower right panel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

Chapter 3: Invariant Representation for the Shape of the Environment ¹⁰

Abstract

Studies have shown that the geometric shape of the surface layout is a primary cue for reorientation, both for rodents (Cheng, 1986) and for humans (Hermer, Spelke & Katsnelson, in press). Are there fundamental differences between representations of environmental layout and representations of other features of the surroundings, such as object locations? Using a disorientation paradigm developed in earlier research (Wang & Spelke, 1997), we measured the relative accuracy of participants' pointing either to multiple objects or to multiple geometric features of the layout (room corners), both before and after they were disoriented. Disorientation had little effect on the coherence of pointing to different room corners, suggesting that humans construct an enduring, static representation of the shape of the layout. In contrast, disorientation significantly reduced the internal coherence of pointing responses to different objects, suggesting that object localization relies primarily on transient, egocentric representations of distinct object positions. Environmental geometry may play a privileged role in reorientation, because its representation is least perturbed by disorientation.

¹⁰ This research is Supported in part by a grant to ESS from NIH (R37-HD 23103). Some of the data was presented in the Sixth Annual Workshop on Object Perception and Memory, Dallas, Nov. 19, 1998. Address correspondence to Ranxiao Wang (francesw@s.psych.uiuc.edu).

A basic question about the nature of spatial representations and navigation processes concerns the kind of reference frames used to specify environmental locations. One navigation strategy is to form representations of the locations of diverse objects and places in an egocentric reference frame, and to update all these representations as the navigator moves or turns. A different strategy is to represent both the navigator's position and the locations of objects and places with respect to something in the world that is stable and independent of the self (allocentric reference frames), and to update only the navigator's position as he or she moves. Although both kinds of representations can guide the spatial behaviors of a mobile observer, they differ in the way information is preserved and processed. Allocentric representations can be stable and enduring, because the locations of objects relative to immobile environmental features does not change over the course of navigation. In contrast, egocentric representations must be dynamic and transient, for the egocentric positions of objects change with every motion of the observer.

Neurophysiological and behavioral studies have demonstrated the existence of multiple forms of egocentric and allocentric representations. For example, neurons in the parietal cortex of monkeys have receptive fields relative to the fovea (Lateral Intraparietal area - LIP), the head (Ventral Intraparietal - VIP), and the arm (Medial Intraparietal - MIP) (Colby & Duhamel, 1996; Duhamel, Colby and Goldberg, 1992). Patients with damage to one side of the parietal cortex may neglect the contralateral side of space relative to a viewer-centered reference frame, an object centered reference frame or an environment-centered reference frame (e.g., Chatterjee, 1994; Drain & Reuter-Loren, 1997; Farah, Brunn, Wong, Wallace & Carpenter, 1990). In behavioral studies, both children and adults show a categorical coding of a target location in a sandbox or a circle, and retrieval of the target is systematically biased toward the categorical mean (Huttenlocher, Hedges & Duncan, 1991; Sandberg, Huttenlocher & Newcombe, 1996; Newcombe, Huttenlocher, Drummey & Wiley, 1998). The alignment of an object array with its surrounding environment (a room or a mat) also influences the retrieval of relative object-to-object orientations (Shelton & McNamara, 1997). The co-existence of multiple representations does not in itself reveal, however, what roles each representation plays in guiding navigation and object localization.

In earlier research, we developed a disorientation paradigm to investigate whether navigation in a relatively novel, small-scale environment depends on an enduring, static cognitive map or on a process of updating transient, egocentric representations (Wang & Spelke, 1997). We assessed participants' pointing to unseen objects both before and after they were disoriented, because dynamic egocentric representations and persisting static representations are affected by disorientation in different ways. If a navigator encodes object locations using an allocentric reference frame and computes the current direction of any object by combining this invariant representation with an estimation of his or her position and orientation, then disorientation will introduce a common error into the localization of all objects, stemming from participants'

mislocalization of the self. Pointing to different objects will remain internally consistent, however, because disorientation will not affect the static representation of object-object relationships. In contrast, if a navigator encodes each object location using an egocentric reference frame, updating the egocentric locations of objects as he or she moves, then disorientation will perturb this updating process and introduce errors into the representation of each object's position. Pointing to different objects therefore will show both absolute and relative errors (internal inconsistencies) after disorientation.

In a series of experiments, Wang & Spelke (1997) found that the internal consistency of pointing to multiple objects was impaired by disorientation. This effect was not due to incidental factors such as time delay, vestibular stimulation, or interfering activities, but rather depended on participants' state of orientation. The effect also was not reversed by reorienting the participants, suggesting that the loss of information about object-object relationships was permanent. The findings provided evidence that humans rely on egocentric representations updated over self motion to locate objects, at least in relatively novel, small-scale environments (see also Farrell & Robertson, 1998; Fukusima, Loomis, & Da Silva, 1997; Loomis, Klatzky, Golledge, Cicinelli, Pellegrino, & Fry, 1993; Presson, & Montello, 1994; Rieser & Rider, 1991).

Further evidence for egocentric representations and updating processes comes from research using a scene recognition paradigm, in which participants were presented first with an array of objects, then the array was occluded, one object was moved, and the array appeared again from the same or a different perspective (Simons & Wang, 1998; Wang & Simons, in press). Participants accurately identified the displaced object when they moved between the first and second presentation and therefore viewed the stationary array from two distinct viewpoints. In contrast, detection of this change was impaired when the participant remained stationary and the array moved between the two presentations so as to produce the same changes in the objects' egocentric positions and orientations. Change detection over self motion was superior to change detection over array motion, even when the surrounding visual background (room walls and furniture) was removed, such that the visual arrays presented in the two conditions were identical. In contrast, change-detection over self motion was impaired when participants were disoriented during their movement from one station point to another. Like the studies of pointing to objects after disorientation, these findings provide evidence that accurate change detection after observer movement depends on an egocentric updating process that predicts the view of a scene from the new vantage point to which one moves.

Nevertheless, the egocentric updating hypothesis raises a question: If environmental locations are encoded relative to the self, how do navigators determine where they are when their egocentric updating mechanism fails and they become disoriented? Common experience, and a wealth of experiments, indicate that disoriented humans and other animals are able to reorient

themselves by observing specific features of their surroundings. For example, Cheng and Gallistel (1984) showed that disoriented rats can use the shape of a box to locate hidden food, but that they fail to use nongeometric 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, in press), as did human adults engaged in an attention-demanding verbal interference task (Hermer et al., in press). 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 nongeometric 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. Conversely, their inability to use the relative positions of distinct objects to reorient or to navigate while disoriented could stem from the fact that such information is more radically impaired by disorientation. The present research investigates these possibilities more directly.

Using the disorientation paradigm described above (Wang & Spelke, 1997), we measured participants' pointing to a set of objects and to a set of geometric features of the layout (room corners), both before and after disorientation. Following Wang & Spelke (1997), we expected that disorientation would reduce the internal consistency of pointing to different objects, providing further evidence that object localization depends on egocentric representations and updating processes. If the representation of environmental geometry depends on the same egocentric updating processes, then its internal consistency also should rely on one's sense of orientation and should be similarly reduced by disorientation. If, on the other hand, geometric features of the layout are represented in a fundamentally different way and so are stable and invariant over observer movement, then disorientation should not impair the internal consistency of pointing to different room corners.

Experiment 1

In this experiment, participants were presented with a rectangular room furnished with four distinct objects arranged in the same angular configuration. Each participant had an objects condition and a corners condition. In each condition, they pointed to the targets (objects and corners, respectively) without vision, both before and after disorientation. For each condition, we obtained three error measures from participants' pointing responses. First, the global, absolute shift in pointing directions relative to true object directions served as a measure of *heading error*, the shift in participants' perceived self-orientation. Second, the inconsistencies between successive points to the same object or corner served as a measure of *pointing error*, or variability in the

behavioral response. Finally and most importantly, the inconsistencies between points to distinct objects or corners served as a measure of *configuration error*. This measure assessed inaccuracies in participants' representation of object-object relationships. If participants form enduring representations of objects or corners, then disorientation should produce an increase in heading error but no increase in configuration error. If participants form transient, egocentric representations of objects or corners, then disorientation should produce an increase both in heading error and in configuration error, above and beyond any increase in pointing error.

Method

Apparatus. The experiment was conducted in a 1.8m X 2.6m rectangular chamber, as shown in Fig. 1. A video camera was mounted at the center of the ceiling to record the pointing responses. Four objects were placed inside the room adjacent to the walls, so that they formed the same angular configuration as the four corners of the room (Figure 1). Participants entered the room through a door at one of the corners. There was a red fabric covering the short wall opposite to the door. Four 40W lights were mounted on the ceiling to illuminate the room. A white noise generator was carried by the experimenter who moved around continuously so as to eliminate any constant auditory cues from any direction.

Design and procedure. Eight Cornell undergraduate students were recruited from a psychology class and received course credit for their participation. Participants entered the chamber with the experimenter and sat down in a swivel chair fixed in the middle of the room. They participated in two conditions—an objects condition and a corners condition—separated by a short break in the room. The order of these two conditions was counterbalanced across participants.

In the objects condition, participants were asked to study the objects so as to remember their locations as accurately as possible, turning around in the chair as needed and taking as long as they wanted. When they reported they were ready, they were asked to close their eyes and point with either hand to the four objects as the experimenter named them. If they made a mistake, they were asked to study the objects again and the initial pointing session was begun anew. After pointing at all the objects correctly, the experimenter blindfolded the participant and turned him or her to face a different, randomly determined orientation. The participant then pointed to the objects as the experimenter named them. Objects were named once in a clockwise order and once in a counterclockwise order, starting randomly from one object. Each participant therefore pointed to each object twice, for a total of 8 pointing responses in this *oriented session*. Then the participant was asked to spin continuously in the chair by pressing his or her feet against the floor, changing direction from time to time on cue from the experimenter, for one minute. The experimenter moved about in the chamber while the participant was turning, to avoid serving as a directional

cue. After the participant stopped, facing in a random direction, the experimenter again named the objects once in a clockwise and once in a counterclockwise order. Each participant again pointed twice to each object in this *disoriented session*.

The corners condition was identical to the objects condition, 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). Participants then proceeded with the four pointing responses at their own pace, and were asked to point again starting with the same corner in the opposite order.

Coding and Data Analysis. The pointing responses of the participants were measured off-line from the TV screen using a radial grid with 10° angular intervals. We calculated the signed error of each pointing response by subtracting the response direction from the true direction of the target (Figure 2). From this measure, we derived three types of errors, as follows.

First, we calculated the overall rotation of a participant’s responses as a measure of his or her *heading error*. To compute this measure, we first averaged the two signed errors to each target (*individual error*) and then computed the mean of the participant’s four individual errors. Heading error should all be 0° when participants are fully oriented, and it should vary randomly between -180° and 180° when they are fully disoriented. Chi square tests on the participants’ heading errors served to assess participants’ state of orientation in each session (Batschelet, 1981; Wang & Spelke, under review). Next, we calculated the consistency of a participant’s different points to the same target within a session as a measure both of the accuracy of participants’ pointing response and of the stability of their representation of target locations within a session. *Pointing error* was computed as the average standard deviation of the two signed errors in successive points to the same object. It should be 0 if participants pointed with full control and with no fluctuations in their spatial representation within a session. Finally and most importantly, we calculated the internal inconsistencies among pointing responses to different targets as a measure of the inaccuracy of the spatial representation. *Configuration error* was computed as the standard deviation of the four individual errors. If the spatial relationship among the four targets was preserved, then the mean direction of pointing to each target should deviate from the true target location by the same amount, yielding a configuration error of 0.

Configuration error is not completely independent of pointing errors. If the representations of individual target positions change within a session, or if participants’ ability to control the direction of their pointing is poor and variable, then the measure of configuration error will be inflated, even if all target positions are perfectly correlated at any given time. To assess the true consistency of participants’ localization of different targets, therefore, the configuration error can be corrected according to the pointing error (Wang & Spelke, under review). A significant increase in configuration error after the correction thus is indicative of inconsistencies in

participants' localization of different targets, over and above any inaccuracies in participants' assessment of self-orientation, participants' control over the pointing response, and participants' ability to maintain a stable spatial representation over the course of a pointing session.

Results

In the oriented sessions of both the objects and the corners conditions, participants maintained their sense of orientation, as indicated by their low heading errors (Chi squares = 29, $p < .0001$; see Figure 3). In the disoriented sessions of the two conditions, participants were effectively disoriented, as indicated by their large and random heading errors (Chi squares < 5.5, $p > .36$; see Figure 3). Pointing error significantly increased after disorientation in the objects condition (paired $t(7) = 2.9$, $p = .023$), but not in the corners condition (paired $t(7) = 1.28$, $p = .24$). Turning to the most important analysis, participants showed a significant increase in configuration error in the disoriented session of the objects condition, relative to the preceding oriented session (paired $t(7) = 4.1$, $p < .005$), even after correcting for the pointing errors (paired $t(6) = 4.0$, $p < .01$).¹¹ In the corners condition, in contrast, configuration error was the same before and after disorientation (paired $t(7) = .16$, $p = .87$; Figure 4). A 2 (condition: objects vs. corners) by 2 (session: oriented vs. disoriented) analysis of variance on the configuration error measure revealed a significant interaction between these factors ($F(1, 14) = 5.2$, $p = .038$). Configuration error was equally low in the two sessions of the corners condition and in the oriented session of the objects condition, and it was reliably higher in the disoriented session of the objects condition.

Discussion

As in Wang and Spelke's experiments, participants who were disoriented pointed to multiple objects not only with a large common error, reflecting errors in their assessment of their own orientation, but also with an increased relative error, reflecting errors in their representation of object-object relationships. The findings of Experiment 1 therefore replicate those of Wang and Spelke (1997), 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 the present study, the increase in configuration error cannot be attributed to fluctuations in participants' represented orientation over the course of a pointing session or to inconsistencies in participants' control over the pointing response, because the inconsistencies in participants' pointing to different objects reliably exceeded the inconsistencies in their pointing to individual objects. The present

¹¹ Because of the sequential retrieval, one subject seemed to have changed the heading estimation between the two sequences, therefore violated the assumption for this analysis and was excluded.

finding therefore provides further evidence that the spatial locations of objects are encoded in an egocentric reference frame and are separately updated over motion of the observer.

In contrast to these findings, participants who were disoriented pointed to multiple corners of the room with a large common error but low relative error. Although the large common error provides evidence that the participants were disoriented in the corners condition as in the objects condition, the low relative error provides evidence that their representation of the shape of the layout survived this disorientation. Experiment 1 therefore provides initial evidence that the overall shape of the layout is encoded as an enduring representation that is unaffected by disorientation.

Nevertheless, it is possible that stimulus or procedural differences between the objects condition and the corners condition account for the differential effects of disorientation. First, one may ask whether the increase in configuration error stems from the fact that the targets in the objects condition are closer to the participants than are the targets in the corners condition. Because any given spatial displacement causes a larger egocentric displacement for a nearby object than for a more distant object, one might propose that participants 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. However, Wang and Spelke (1997) tested participants' pointing to objects that were outside the test chamber and considerably farther away than the objects or corners in Experiment 1, and obtained measures of configuration error as high as in the objects condition of the present study. We conclude, therefore, that differences in the egocentric distances of the objects and corners fails to account for the difference in configuration error observed when pointing to objects vs. corners.

A second difference between the objects condition and the corners condition concerns the spatial properties of the targets. Corners project one-dimensional images in the visual scene: they have vertical but no horizontal extent. As a result, a participant 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 participant can point accurately to an object by aiming to different horizontal locations (e.g., its center vs. its right border). This difference raises the possibility that disorientation brought about an inconsistency in participants' 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 vs. 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 vs. corners conditions, three further differences between these conditions indeed may have contributed to the differences in participants' performance. First, the robustness of the representation of the room corners over disorientation may be due to our use of a highly salient symmetric configuration. Although both the room corners and the objects were arranged in the same angular 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 participants' memory for the corner relationships and guided participants' pointing to corners throughout the experiment, e.g. by inducing a strategy of separating all alternate points by 180°, thus reducing configuration error in the corners condition. Second, participants 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), encouraged participants to attend to the target configuration in the corners condition more than in the objects condition. Experiment 2 was undertaken to test all these possibilities against the alternative hypothesis that objects and room corners are encoded in different reference frames.

Experiment 2

Like Experiment 1, Experiment 2 compared participants' 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, participants 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 vs. corners, observed in Experiment 1, stemmed from the use of a salient symmetrical room, of identical corners but different objects, or of differing verbal instructions in the objects vs. corners condition, then this difference should disappear in Experiment 2. On the other hand, if the difference reflects the egocentric updating process for objects and an static representation for corners, then the same pattern should be observed as in Experiment 1: Disorientation should produce high configuration error in pointing to objects but low configuration error in pointing to corners.

Method

Apparatus. The experiment was conducted in a large, irregularly shaped room furnished with tables, a couch, cabinets, a sink and counter, and other objects (see Figure 5). Four small, identical chairs were arranged into the same configuration as the corners of the room, in a different orientation and closer to the participant (Figure 5). A video camera mounted above the swivel chair recorded the pointing responses. The room was illuminated by lighting on the ceiling. As in Experiment 1, the experimenter carried a white noise generator and moved about continuously to avoid any auditory directional cues.

Design and procedure. Eight MIT undergraduate students participated in this study and each received \$2 in compensation. Each participant pointed to the objects in one session and to the room corners in another session, in an order that was counterbalanced across participants. No objects or corners were named during the pointing sessions; instead, the participants 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 1.

Results

In both the objects and the corners conditions, participants showed low heading errors in the oriented sessions (Chi squares = 38, $p < .0001$) and high, random heading errors in the disoriented sessions, indicating that they were effectively disoriented (Chi squares < 2.4, $ps > .66$; see Figure 6). Pointing errors did not differ in either the objects condition or the corners condition (paired $t(7) < 1.6$, $ps > .16$). The configuration error significantly increased after disorientation when participants pointed to chairs (paired $t(7) = 3.3$, $p = .01$), even after correcting for the pointing errors ($t(7) = 4.5$, $p = .003$), but it did not increase significantly when participants pointed to corners (paired $t(7) = 1.5$, $p = .18$). There was a significant interaction ($F(1,14) = 7.6$, $p = .015$) (see Figure 7).

Discussion

The findings of Experiment 2 replicated closely those of Experiment 1. As in that experiment, disorientation had equal effects on the accuracy of participants' perception of their own heading when they pointed to corners vs. objects, but differential effects on participants' representation of the relationships among the targets to which they pointed. When participants 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 participants pointed to corners, in contrast, disorientation led to no increase in configuration error, providing evidence for static, enduring representations for corner locations that persisted

over disorientation. This difference in pointing to objects vs. corners was obtained even though the room was not symmetrical, the targets were homogeneous, and the instructions were identical in the two conditions. Even in an irregular room, therefore, the shape of the layout appears to be encoded independently of self-orientation. Moreover, even when objects are identical, their positions appear to be encoded and updated separately, and this representation is dependent on self-orientation.

General Discussion

In two experiments, we tested the relative accuracy of pointing to multiple objects and to corners of a room before and after disorientation. Relative pointing errors significantly increased after disorientation in the objects condition, but not in the corners condition, even when the objects were identical and the room was irregular. These data suggest that different mechanisms are involved in the representation of environmental geometry and individual objects. Although the shape of the layout is encoded in the form of an enduring representation that is independent of self-orientation, the locations of objects are encoded in separate, transient representations that depend on self-orientation and therefore are impaired by disorientation.

In Experiment 2, the differences in participants' representations of objects vs. corners were obtained despite the close similarity between the objects and corners conditions. Even when we used exactly the same pointing task, the same disorientation procedure, the same geometric arrangement of targets, and the same measurement of configuration error, the representation of the room geometry remained accurate over disorientation whereas the representation of object locations was significantly impaired. These findings provide further evidence that the impairment caused by disorientation is not due to extraneous factors such as the pointing task, the specific measurements taken, or general limits on memory. Rather, it appears that the nature of the underlying spatial representations and the processes by which they are used determines when the internal consistency is preserved and when it is reduced.

The evidence for egocentric updating and invariant, static representations in the current studies was obtained using a task requiring accurate spatial knowledge. It's very likely that some qualitative, coarse representation of the same environment is formed at the same time. Moreover, egocentric updating and invariant, allocentric maps are not the only two alternatives. In particular, although an allocentric map itself is a static representation by nature, egocentric representations can be either dynamic or static (e.g., 'snapshots' and view-dependent representations). As an allocentric cognitive map, a static egocentric representation can be stored in long term memory and retrieved to compute the current target positions. In the paradigm used in our studies, static egocentric representations make similar predictions as static allocentric representations; thus the current studies suggest that in a relatively small, novel environment object locations are encoded in

an egocentric reference frame and updated according to observer movements, while representation of the shape of the surroundings is static, either allocentric or view-dependent.

There are two serious limitations for an egocentric updating system. The first one is the limitation of capacity. It seems very implausible for any intelligent navigators to employ egocentric updating as the only mechanism and maintain on-line all known locations. As the set of learned locations becomes larger and larger, the energy and time required for on-line updating increase, and this mechanism seems less and less efficient. The second limitation concerns the scale of the environment. Adding vectors to an already very large vector (e.g., for distant targets) has little influence on it, thus it does not make much sense to update target locations not in the current environment. Obviously one needs an alternative mechanism to compensate for the egocentric updating system. One possible solution is the pairing of an egocentric updating system and static egocentric representations. For example, one can simply stop updating the egocentric representations of the current environment whenever s/he moves to a different environment, and leave the current egocentric measurements as they are, until s/he enters the same environment again. The egocentric measurements left behind in the background are therefore static, long term memories. In this sense, egocentric updating and view-dependent representations are two parts of a larger navigation system. Although current studies fail to provide evidence for static egocentric representation of objects locations, one may need to study larger scale environments and cases of switching local environments to understand more complicated navigation tasks.

Why do we form an enduring, static representation of environmental shape but a transient, egocentric representation of object locations? One possibility appeals to our evolutionary history and to the purposes that spatial representations serve. 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. Future experiments could test each of these possibilities. For example, it will be interesting to study the nature of representations of an array consisting of a single object, or 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 accord with the geometry of the layout. In order for a disoriented person or animal to reestablish his position and heading in the layout, the person or animal 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.

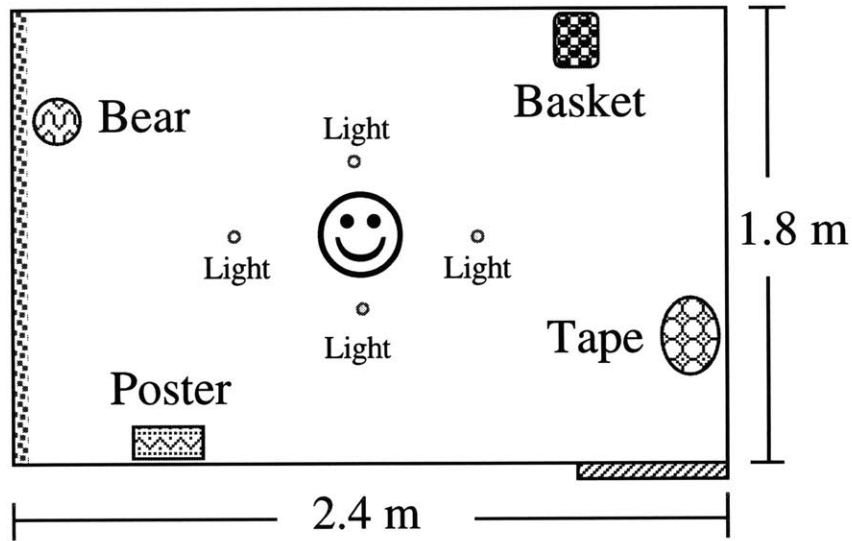


Figure 1. An overhead view of the rectangular room for Experiment 1. Four small objects (a toy bear, a basket, a poster, and a video tape) were placed against the walls so as to form the same angular configuration as the four corners, in a different orientation. Four 40W lights were mounted on the ceiling symmetrically to illuminate the room. A swivel chair was fixed to the ground in the middle of the room, and a video camera was mounted at the center of the ceiling to send the image to a VCR outside of the room and to record the pointing responses.

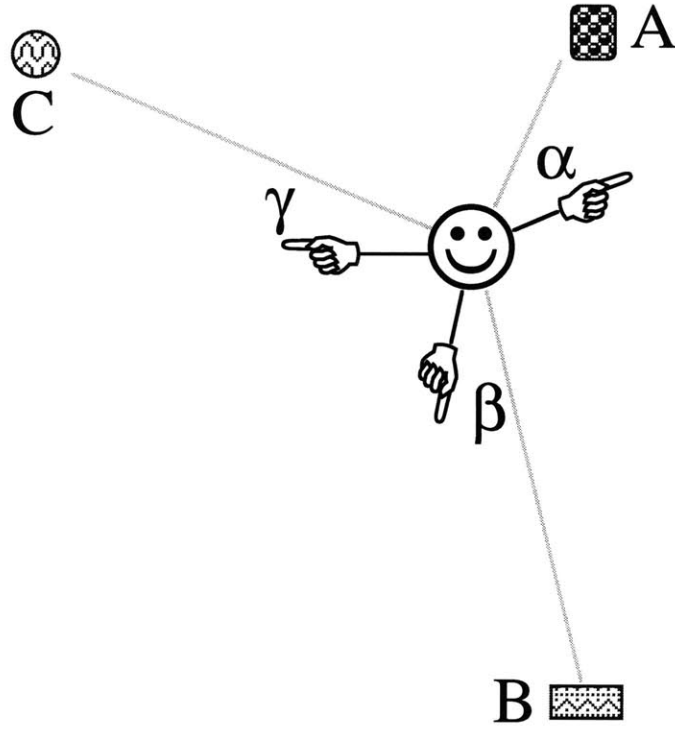


Figure 2. An illustration of the data analysis. Suppose there are three targets A, B and C around the observer, shown in an overhead view. The individual errors are the angular difference between the pointing direction (shown by a hand) and the true direction of the target (α , β , γ , respectively). The *heading error* is calculated as the mean of the individual errors $(\alpha+\beta+\gamma)/3$. The *pointing error* is calculated as $[\text{stdev}(\alpha_1, \alpha_2) + \text{stdev}(\beta_1, \beta_2) + \text{stdev}(\gamma_1, \gamma_2)]/3$. The *configuration error* is calculated as the standard deviation of the three individual errors.

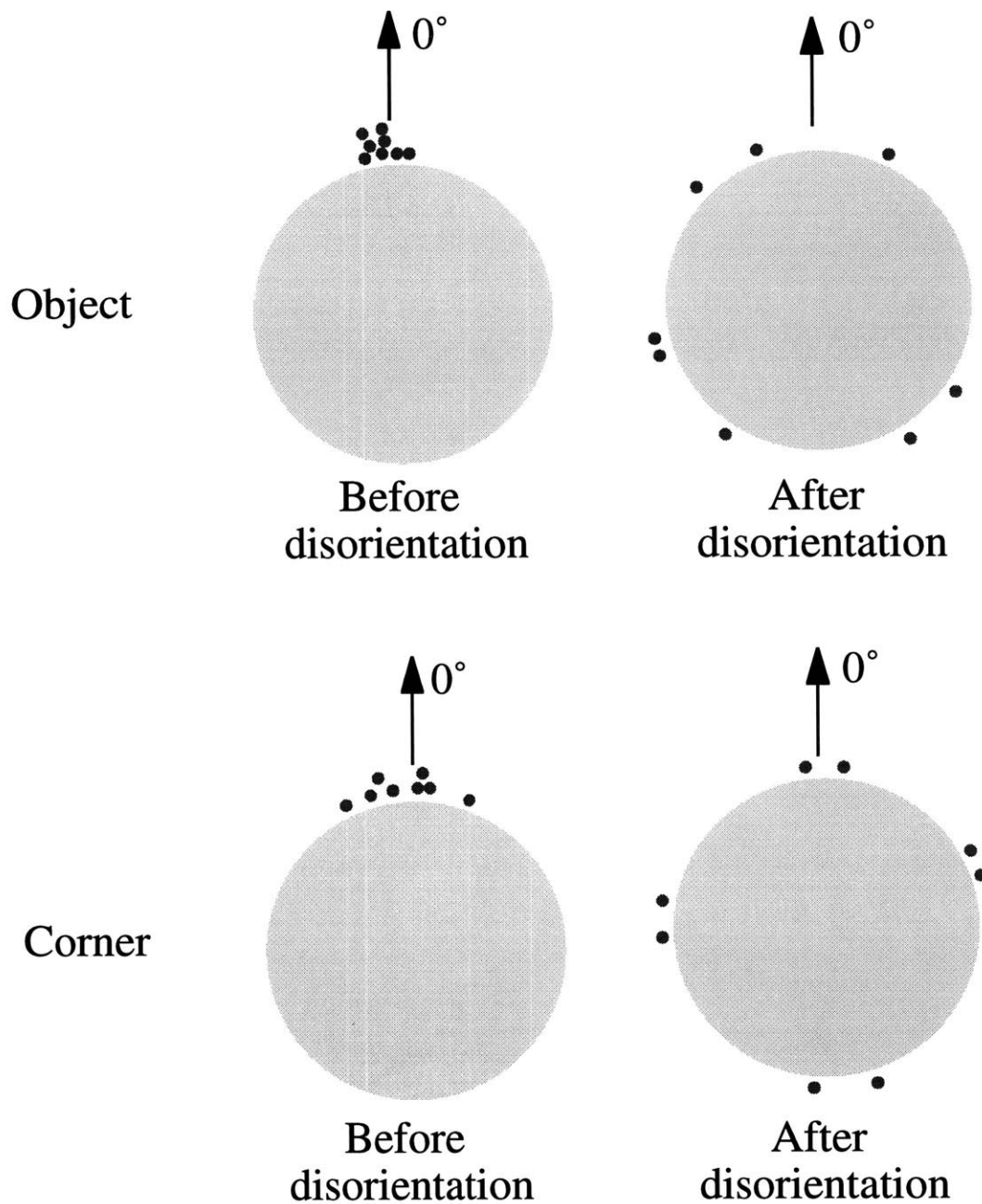


Figure 3. The heading error in Experiment 1, in the object condition before disorientation (upper left panel), the object condition after disorientation (upper right panel), the corner condition before disorientation (lower left panel) and the corner condition after disorientation (lower right panel). The arrow indicates the correct orientation (0° rotation) and each dot represents the overall rotation of one participant in that condition. Clustered dots around 0° indicated that participants were oriented, whereas random distribution of the dots around the circle indicated they were disoriented.

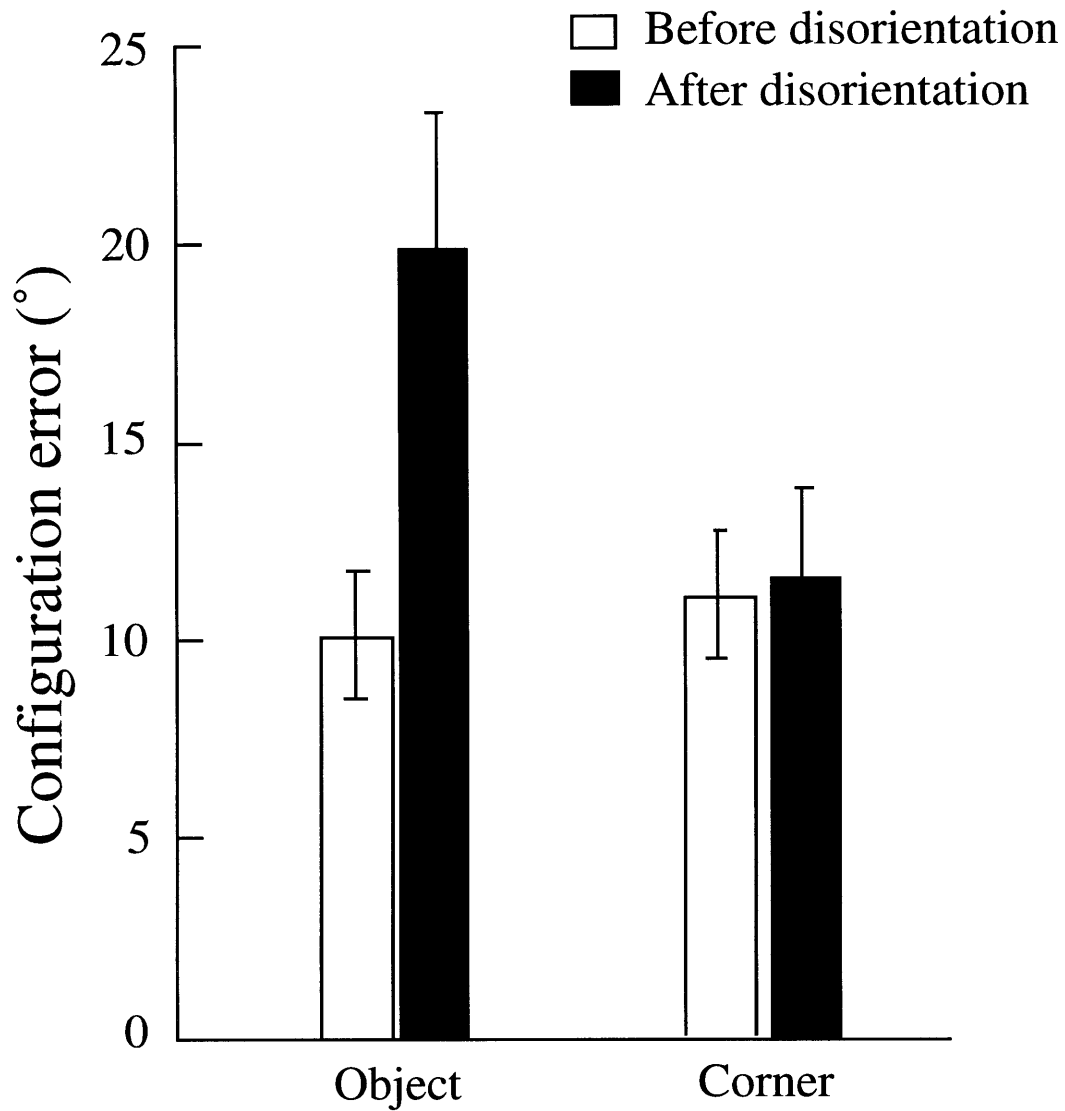


Figure 4. The configuration errors in Experiment 1. The error bars are standard errors.

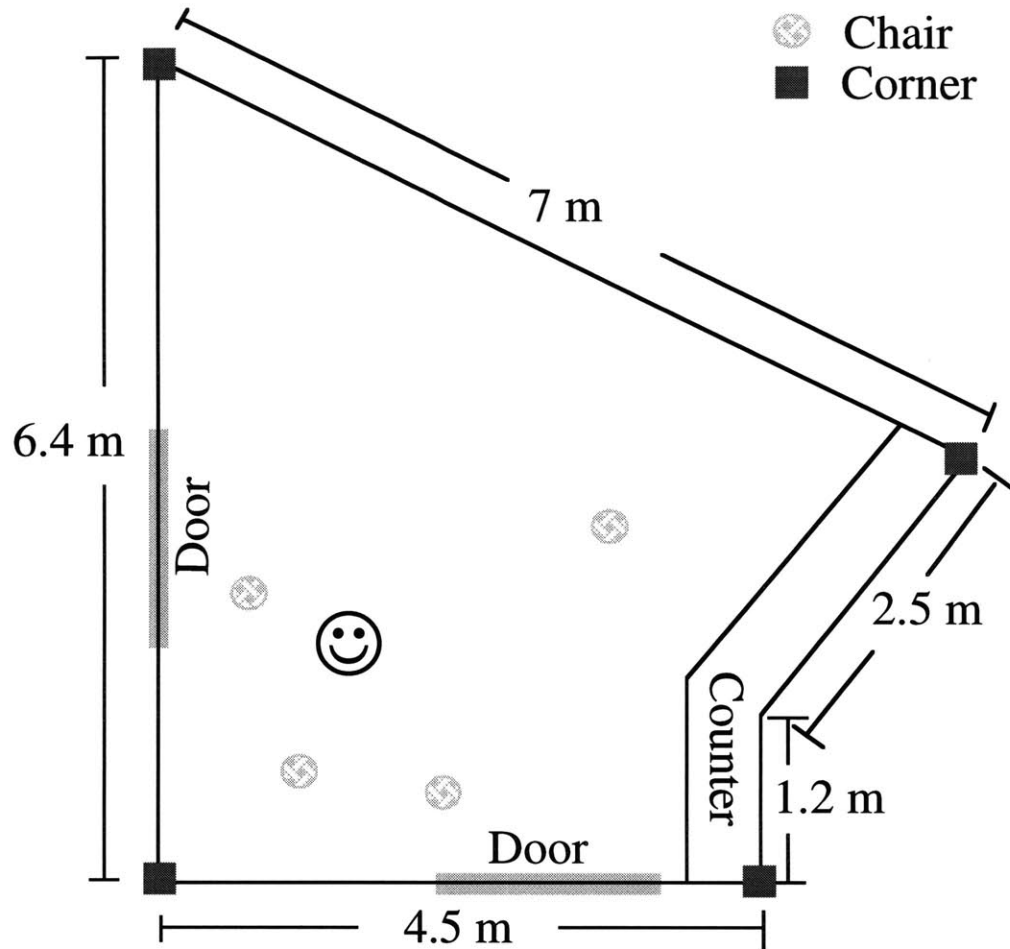


Figure 5. An overhead view of the irregular room for Experiment 2. Four small chairs were placed inside the room and formed the same configuration as the four corners, in a different orientation. The room was illuminated by lights on the ceiling. The swivel chair was fixed to the ground, and a video camera was mounted above the chair on the ceiling to record the pointing responses.

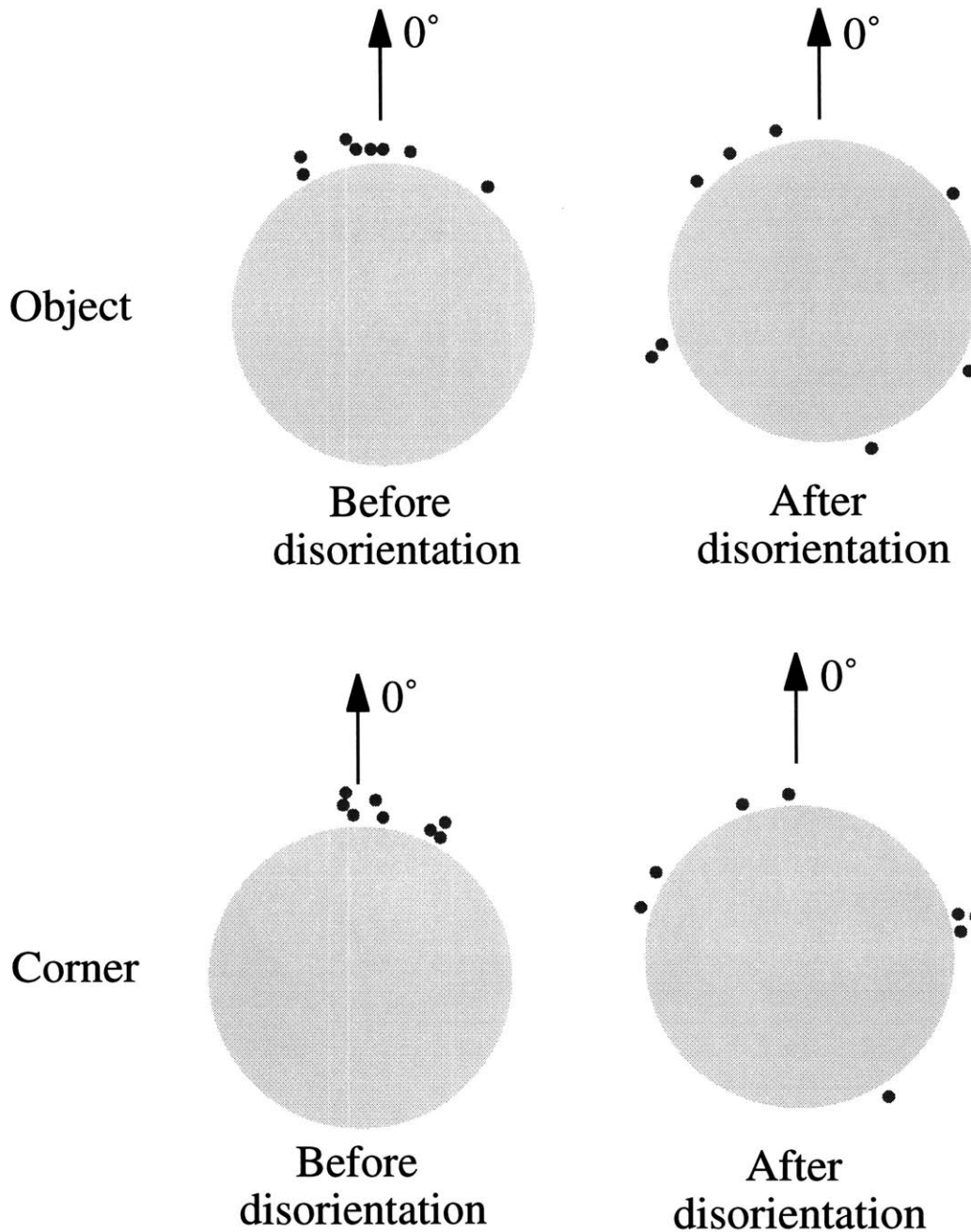


Figure 6. The heading error in Experiment 2, in the object condition before disorientation (upper left panel), the object condition after disorientation (upper right panel), the corner condition before disorientation (lower left panel) and the corner condition after disorientation (lower right panel). The arrow indicates the correct orientation (0° rotation) and each dot represents the overall rotation of one participant in that condition. Clustered dots around 0° indicated that participants were oriented, whereas random distribution of the dots around the circle indicated they were disoriented.

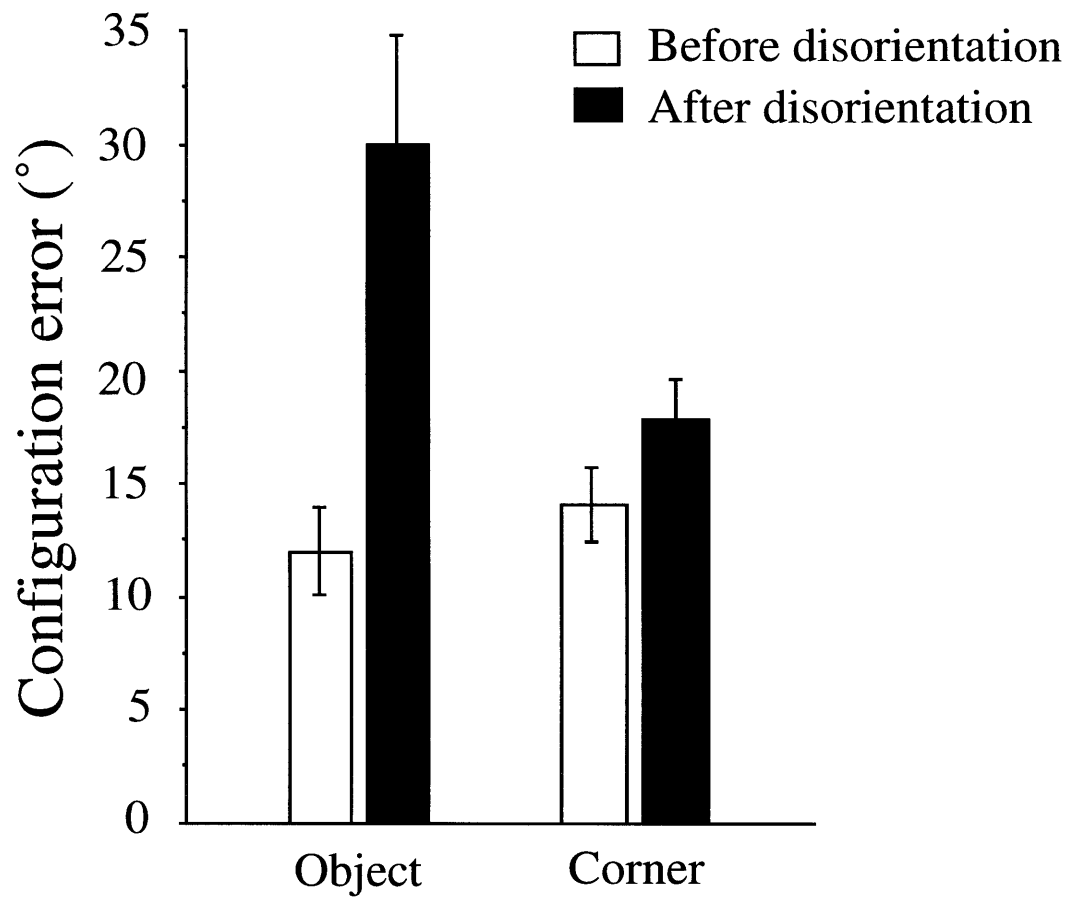


Figure 7. The configuration errors in Experiment 2. The error bars are standard errors.

References

- Batschelet, E. (1981). *Circular statistics in biology*. Academic press: London.
- Bennett, A. T. D. (1996). Do animals have cognitive maps? *Journal of Experimental Biology*, **199**, 219-224.
- Berthoz, A., Israel, I., Francois, P. G., Grasso, R. and Tsuzuku, T. (1995). Spatial memory of body linear displacement: What is being stored? *Science*, **269**, 95-98.
- Biegler, R. & Morris, R. G. M. (1993). Landmark stability is a prerequisite for spatial but not discrimination learning. *Nature*, **361**, 631-633.
- Biegler, R. & Morris, R. G. M. (1996). Landmark stability: Studies exploring whether the perceived stability of the environment influences spatial representation. *The Journal of Experimental Biology*, **199**, 187-193.
- Chatterjee, A. (1994). Picturing unilateral spatial neglect: Viewer versus object centered reference frames. *Journal of Neurology, Neurosurgery & Psychiatry*, **57**, 1236-1240.
- Cheng, K. & Gallistel, C. R. (1984). Testing the geometric power of an animal's spatial representation. In H. L. Roitblat, T. G. Bever, and H. S. Terrace (Eds.), *Animal Cognition* (p. 409-423). Hillsdale, NJ: Erlbaum.
- Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition*, **23**, 149-178.
- Colby, C. L. & Duhamel, J.-R. (1996). Spatial representations for action in parietal cortex. *Cognitive Brain Research*, **5**, 105-115.
- Collett, T. S. (1996). Insect navigation *en route* to the goal: multiple strategies for the use of landmarks. *Journal of Experimental Biology*, **199**, 227-235.
- Diwadkar, V. A., & McNamara, T. P. (1997). Viewpoint dependence in scene recognition. *Psychological Science*, **8**, 302-307.
- Drain, M., Reuter-Loren, P. A. (1997). Object-centered neglect for letters: Do informational asymmetries play a role? *Neuropsychologia*, **35**, 445-456.
- Dudchenko P. A. & Taube, J. S. (1997). Correlation between head direction cell activity and spatial behavior on a radial arm maze. *Behavioral Neuroscience*, **111**, 3-19.
- Dudchenko, P. A., Goodridge, J. P. & Taube, J. S. (1997). The effects of disorientation on visual landmark control of head direction cell orientation. *Experimental Brain Research*, **115**, 375-380. (a)
- Dudchenko, P. A., Goodridge, J. P., Seiterle, D. A. & Taube, J. S. (1997). Effects of repeated disorientation on the acquisition of spatial tasks in rats: dissociation between the appetitive radial arm maze and aversive water maze. *Journal of Experimental Psychology: Animal Behavior Processes*, **23**, 194-210. (b)
- Duhamel, J.-R., Colby, D. L. & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, **255**, 90-92.
- Dyer, F. C. (1996). Spatial memory and navigation by honeybees on the scale of the foraging range. *Journal of Experimental Biology*, **199**, 147-154.
- Etienne, A. S., Maurer, R. & Sguinot, V. (1996). Path integration in mammals and its interaction with visual landmarks. *Journal of Experimental Biology*, **199**, 201-209.
- Farah, M. J., Brunn, J. L., Wong, A. B., Wallace, M. A. & Carpenter, P. A. (1990). Frames of reference for allocating attention to space evidence from the neglect syndrome. *Neuropsychologia*, **28**, 335-348.
- Farrell, M. J. & Robertson, I. H. (1998). Mental rotation and the automatic updating of body-centered spatial relationships. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, **24**, 227-233.
- Fukushima, S. S., Loomis, J. M., & Da Silva, J. A. (1997). Visual perception of egocentric distance as assessed by triangulation. *Journal of Experimental Psychology: Human Perception and Performance*, **23**, 86-100.
- Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT Press.

- Goodridge, J. P. & Taube, J. S. (1995). Preferential use of the landmark navigational system by head direction cells in rats. *Behavioral Neuroscience*, **109**, 49-61.
- Gothard, K. M., Skaggs, W. E. & McNaughton, B. L. (1996). Dynamics of mismatch correction in the hippocampal ensemble code for space: Interaction between path integration and environmental cues. *The Journal of Neuroscience*, **16**, 8027-8040.
- Hermer, L. & Spelke, S. S. (1994). A geometric process for spatial reorientation in young children. *Nature*, **370**, 57 - 59
- Hermer, L. & Spelke, S. S. (1996). Modularity and development: the case of spatial reorientation. *Cognition*, **61**, 195-232.
- Hermer, L. (1997). Internally coherent spatial memories in a mammal. *Neuroreport*, **8**, 1743-1747.
- Hermer, L., Spelke, S. S. & Katsnelson, (in press). Sources of flexibility in human cognition: Dual-task studies of space and language. *Cognitive Psychology*.
- Hermer-Vazquez, L. (1997). Cognitive flexibility as it emerges over development and evolution : the case of two navigational tasks in humans. Ph. D. thesis at Cornell University, Aug., 1997.
- Huttenlocher, J., Hedges, L. V., & Duncan, S. (1991). Categories and particulars: Prototype effects in estimating spatial location. *Psychological Review*, **98**, 352-376.
- Knierim, J. J., Kudrimoti, H. S. & McNaughton, B. L. (1995). Place cells, head direction cells, and the learning of landmark stability. *Journal of Neuroscience*, **15**, 1648-1659.
- Levinson, S. C. (in press). The role of language in everyday human navigation.
- Loomis, J. M., Klatzky, R. L., Golledge, R. G., Cicinelli, J. G., Pellegrino, J. W., & Fry, P. A. (1993). Nonvisual navigation by blind and sighted: Assessment of path integration ability. *Journal of Experimental Psychology: General* , **122**, 73-91.
- Margules J. & Gallistel, C. R. (1988). Heading in the rat: determination by environmental shape. *Animal Learning*, **16**, 404-410.
- Martin, G. M., Harley, C. W., Smith, A. R., Hoyles, E. S. & Hynes, C. A. (1997). Spatial disorientation blocks reliable goal localization on a plus maze but does not prevent goal localization in the Morris maze. *Journal of Experimental Psychology: Animal Behavior Processes*, **23**, 183-193.
- McNaughton, B. L., Knierim, J. J. & Wilson, M. A. (1995). Vector encoding and the vestibular foundations of spatial cognition: neurophysiological and computational mechanisms. In M. Gazzaniga (ed.) *The Cognitive Neurosciences* , Boston: MIT Press, 585-595.
- Mittelstaedt, M. L. & Mittelstaedt, H. (1980). Homing by path integration in a mammal. *Naturwissenschaften*, **67**, 566-567.
- Muller, M. & Wehner, R. (1988). Path integration in desert ants. *Proceeding of National Academy of Science USA*, **85**, 5287-5290.
- Muller, R. U. & Kubie, J. L. (1987). The effects of changes in the environment on the spatial firing of hippocampal complex-spike cells. *Journal of Neuroscience*, **77**, 1951-1968.
- Newcombe, N., Huttenlocher, J., Drummey, A. B., & Wiley, J. G. (1998). The development of spatial location coding: Place learning and dead reckoning in the second and third years. *Cognitive Development*, **13**, 185-200.
- O'Keefe, J. & Burgess, N. (1996). Geometric determinants of the place fields of hippocampal neurons. *Nature*, **381**, 425-428.
- O'Keefe, J. & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford: Clarendon.
- O'Keefe, J. & Speakman, A. (1987). Single unit activity in the rat hippocampus during a spatial memory task. *Experimental Brain Research*, **68**, 1-27.
- O'Keefe, J. and Burgess, N. (1996). Geometric determinants of the place fields of hippocampal neurons. *Nature*, **381**, 425-428.
- Presson, C. C. & Montello, D. R. (1994). Updating after rotational and translational body movements: coordinate structure of perspective space. *Perception*, **23**, 1447-1455.
- Quirk, G. J., Muller, R. U. & Kubie, J. L. (1990). The firing of hippocampal place cells in the dark depends on the rat's recent experience. *Journal of Neuroscience*, **10**, 2008-2017.
- Rieser, J. J. & Rider, E. A. (1991). Young children's spatial orientation with respect to multiple targets when walking without vision. *Developmental Psychology*, **27**, 97-107.

- Roskos-Ewoldsen, B., McNamara, T. P., Shelton, A. L., & Carr, W. (1998). Mental representations of large and small spatial layouts are orientation dependent. *Journal of Experimental Psychology: Learning Memory and Cognition*, **24**, 215-226.
- Sandberg, E. H., Huttenlocher, J., & Newcombe, N. (1996). The development of hierarchical representation of two-dimensional space. *Child Development*, **67**, 721-739.
- Shelton, A. L. & McNamara, T. P. (1997). Multiple views of spatial memory. *Psychonomic Bulletin & Review*, **4**, 102-106.
- Shelton, A. L., & McNamara, T. P. (1997). Representing space: Reference frames and multiple views. *Proceedings of the 19th Annual Conference of the Cognitive Science Society, Stanford University, Aug 7-10, 1997*. p1048.
- Sholl, M. J. (1987). Cognitive maps as orienting schemata. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, **13**, 615-628.
- Simons, D. J. & Wang, R. F. (1998). Perceiving real-world viewpoint changes. *Psychological Science*, **9**, 315-320.
- Srinivasan, M. V., Zhang, S. W., Lehrer, M. & Collett, T. S. (1996). Honeybee navigation *en route* to the goal: visual flight control and odometry. *Journal of Experimental Biology*, **199**, 237-244.
- Sutherland, R. J. & Dyck, R. H. (1984). Place navigation by rats in a swimming pool. *Canadian Journal of Psychology*, **38**, 322-347.
- Tarr, M. J. (1995). Rotating objects to recognize them: A case study on the role of viewpoint dependency in the recognition of three-dimensional objects. *Psychonomic Bulletin & Review*, **2**, 55-82.
- Tarr, M. J., & Pinker, S. (1989). Mental rotation and orientation-dependence in shape recognition. *Cognitive Psychology*, **21**, 233-282.
- Tarr, M. J., Bülthoff, H. H., Zabinski, M. & Blanz, V. (1997) To what extent do unique parts influence recognition across changes in viewpoint? *Psychological Science*, **8**, 282-289.
- Taube, J. S. & Burton, H. L. (1995). Head direction cell activity monitored in a novel environment and during a cue conflict situation. *Journal of Neurophysiology*, **74**, 1953-1971.
- Taube, J. S., Goodridge, J. P., Golob, E. J., Dudchenko, P. A. & Stackman, R. W. (1996). Processing the head direction cell signal: A review and commentary. *Brain Research Bulletin*, **40**, 477-486.
- Taube, J. S., Muller, R. U. & Ranck, J. B. (1990). Head-direction cells recorded from the postsubiculum in freely moving rats. *The Journal of Neuroscience*, **10**, 436-447
- Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, **55**, 189-208.
- Wang, R. F. & Simons, D. J. (in press). Active and passive scene recognition across views. *Cognition*.
- Wang, R. F. & Spelke, E. S. (1997). Humans rely on egocentric representations for accurate spatial navigation. *Proceedings of the 19th Annual Conference of the Cognitive Science Society, Stanford University, Aug 7-10, 1997*. p1083.
- Wang, R. F., Hermer, L. & Spelke, E. S. (in press). Mechanisms of reorientation and object localization by human children: a comparison with rats. *Behavioral Neuroscience*.
- Wehner R. & Srinivasan M. V. (1981). Searching behavior of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *Journal of comparative Physiology*, **142**, 315-318.
- Wiener, S. I., Paul, C. A. & Eichenbaum, H. (1989). Spatial and behavioral correlates of hippocampal neuronal activity. *The Journal of Neuroscience*, **9**, 2737-2763.
- Wilson, M. A. & McNaughton, B. L. (1993). Dynamics of the hippocampal ensemble code for space. *Science*, **261**, 1055-1057.