

Individual and Strategy Differences in an Allocentric-Heading Recall Task

Heather Burte (burte@psych.ucsb.edu)

Department of Psychological & Brain Sciences, UCSB
Santa Barbara, CA 93106 USA

Mary Hegarty (hegarty@psych.ucsb.edu)

Department of Psychological & Brain Sciences, UCSB
Santa Barbara, CA 93106 USA

Abstract

Participants estimated allocentric headings using pictures of familiar buildings around a college campus, in an allocentric-heading recall task. A weak relationship between sense-of-direction and accuracy, an alignment effect, and a novel relationship between strategy and accuracy were found. These results demonstrate that sense-of-direction and strategy use differentially affect accuracy across heading disparities. Our findings suggest that individual differences and strategy differences need to be incorporated into current hypotheses regarding allocentric-heading – specifically, into the animal-model hypothesis.

Keywords: allocentric heading; sense of direction; heading-recall; strategy; egocentric and allocentric reference frames.

Introduction

People characterize their ability to move effectively through environmental-scale spaces, such as neighborhoods or cities, by referring to their ‘sense-of-direction’. Kozlowski and Bryant (1977) found that people’s ratings of their sense-of-direction (or SOD) correlated with accuracy in distance, direction, and time estimation tasks. Since then, research has either focused on how to assess SOD or how SOD correlates with performance in environmental-scale spatial tasks (e.g., Hegarty et al., 2002). However, the field is lacking insights into the underlying causes of the vast individual differences found in environmental-scale spatial cognition.

Research on SOD has typically focused on strategy differences in navigation or on individual differences in learning novel environments. In terms of strategy differences, individuals with a poor SOD tend to prefer route strategies and those with a good SOD tend to prefer survey strategies (Prestopnik & Roskos-Ewoldsen, 2000). In terms of individual differences, there are large individual differences in the rates and accuracy with which individuals can learn novel environments and these differences are related to self-reported SOD (Ishikawa & Montello, 2006).

To date, little research has focused on strategy and individual differences in manipulating one’s knowledge of familiar environments; however, manipulating one’s spatial knowledge is essential for wayfinding and route planning. Research that has used familiar environments tends to focus on two tasks: egocentric pointing (pointing from one’s current location towards a landmark) and judgments of relative direction (pointing from an imagined location and orientation towards another landmark) (e.g. Kozlowski &

Bryant, 1977; Hegarty et al., 2002). These studies found significant correlations between SOD and task performance, but have not investigated strategy differences.

The strategies identified during navigation, namely route and survey strategies, are not necessarily relevant in all spatial knowledge manipulation tasks (such as egocentric pointing and judgments of relative direction tasks). Therefore, research is needed to uncover the strategies used in spatial knowledge manipulation tasks – specifically, in environmental-scale spaces. In contrast, research on strategy differences has tended to utilize small-scale tasks. Kozhevnikov and Hegarty (2001) found that when people complete judgments of relative direction tasks, while viewing a map, they use either perspective-taking or mental rotation strategies. They found individual differences in performance, which were related to SOD, and they identified two strategies, which were separable abilities.

The goal of this paper is to investigate the individual and strategy differences that exist within manipulating one’s environmental-scale spatial knowledge. To do so, we will focus on one task, the allocentric-heading recall task (Sholl, Kenny, & DellaPorta, 2006), which requires participants to manipulate their spatial knowledge of a familiar place.

Sholl et al. (2006) developed the allocentric-heading recall task to reveal the architecture of a proposed human head-direction system. They argued that SOD is a single-faceted construct related to the performance of a head-direction system in humans, and they assumed that this system operated similarly to the head-direction system found in rats (Ranck, 1984). In rats, each head-direction cell fires maximally to one angle of difference between the rat’s facing direction and a reference direction grounded in the environment. In other words, head-direction cells respond to allocentric headings and not directions based on the axis of the body (or egocentric headings). Sholl et al. proposed that the human head-direction system operates similarly to that of rats and that the human head-direction system is the neural mechanism underlying self-reported SOD. We will refer to this the animal-model hypothesis.

In the allocentric-heading recall task, participants view photographs of a familiar environment, identify the direction from which the photographs were taken, and then rotate in their chair to reproduce the direction. Initial studies (Sholl et al., 2006) revealed an alignment effect. Specifically, when a participant is facing the same direction as that from which the photograph was taken, participants

were more accurate (a facilitation effect). However, when participants were 180° misaligned from the direction of the photograph (for example, they faced north but the photograph was taken from a south-facing direction), participants were the least accurate (a detrimental effect). The alignment effect was explained as interference between one's current head-direction signals and the retrieval of the head-direction signals, which were activated when the individual viewed the photograph location in the real world. Strong correlations (.7 or higher) between performance on the allocentric-heading task and self-assessed ratings of SOD supported Sholl et al.'s proposal that SOD solely reflects the operation of the human head-direction system.

The allocentric-heading recall task assesses people's ability to manipulate their spatial knowledge of environmental-scale spaces. According to Sholl et al., when viewing a building, the allocentric-heading of that view is stored in memory and is linked to signals of body-direction. Upon seeing a picture of that building, a person recognizes the building, and then recalls the allocentric-heading from spatial memory. Therefore, Sholl et al. proposed that only one strategy exists, and individual differences reflect differences in the fidelity of head-direction signals, and consequently, the ability to carry out this strategy.

In contrast to this view, Burte and Hegarty (2012) found preliminary evidence for possible strategy differences. During informal debriefing interviews, participants reported a range of strategies, including imaging a walk to the photograph location, and relating the photograph heading to the direction of a local mountain range. However, strategy differences have yet to be systematically investigated in this task.

There is also a possibility that familiarity with the tested environment drives individual differences in performance. Sholl et al. did not investigate familiarity differences, as pre-testing had revealed that all their pictures were highly familiar to participants. However, Burte and Hegarty (2012) found significant correlations between familiarity and SOD, as well as between familiarity and accuracy, despite pre-testing photos for high familiarity. This suggests that individual differences in this task might be partially due to differences in familiarity with the environment.

The main purpose of this study is to investigate individual and strategy differences within the allocentric-heading recall task. First we will describe the allocentric-heading task in more detail and then consider strategy differences found within a similar task.

Allocentric-Heading Recall Task

The allocentric-heading recall task is a four-alternative, forced-choice task, using campus pictures as stimuli. Pictures were taken from magnetic north, east, south or west (to match the intrinsic structure of the environment). However, while cardinal directions will be used for simplicity in writing this article, it should be noted that cardinal directions were never used in written or verbal instructions, as they are not required to complete the task.

First, we will define key terminology used: *picture heading* is the photographer's orientation when taking the picture; *default heading* is the orientation of participant before each trial; *response heading* is the orientation the participant responded with; and *heading disparity* is the angular disparity between default heading and picture heading. The animal-model hypothesis makes predictions about the relationship between heading disparities and performance – specifically, about the alignment effect; therefore, heading disparity is the main independent measure of interest.

Turning in one's chair (to replicate the picture heading) was used as the response mode in previous studies. Sholl et al. (2006) argued that turning to represent an angle was a natural response for this task, because turning allows for one's current head-direction cells to find a match to the memory of one's head-direction cell firing. A secondary goal of this study was to investigate whether participants could perform this task without rotating in a chair, but only by using a button-press as the response mode. Therefore, we attempted to replicate Sholl et al.'s results with an alternative, less body-based response mode.

Strategy Differences

In studies using a judgments of relative direction task (JRDs), a dissociation has been made between two strategies: (1) a *perspective-taking strategy* whereby participants imagined moving themselves to assume a new orientation, or used directions related to their bodies to assume a new orientation; and (2) a *mental rotation strategy* whereby participants imagined moving the entire scene around themselves, or imagined rotating angles between locations (Kozhevnikov & Hegarty, 2001). This suggests that participants can think in terms of a body-based reference frame (*egocentric*), or a reference frame grounded in the environment (*allocentric*) while completing the task.

Kozhevnikov, Motes, Rasch, and Blajenkova (2006) found that the perspective-taking strategy resulted in decreased accuracy with increasing heading disparities, a similar pattern to that found by Sholl et al. (2006). However, use of a mental rotation strategy resulted in a significantly weaker alignment effect. Therefore, another goal of this study is to investigate if these strategy differences exist within the allocentric-heading recall task.

In sum, our goals are (1) to investigate if the predictions of the animal-model hypothesis are robust to a new context and to a button-press response mode; (2) to investigate our prediction that individual differences in familiarity are related to task performance; (3) to determine if egocentric and allocentric strategy use exist within this task; (4) to investigate if individual differences in SOD and strategy are related to task performance; and (5) to investigate whether strategy differences are related to SOD.

Method

Participants Seventy-four students (39 males and 35 females) participated as part of a research requirement. Two

participants, both males, were excluded from analysis because their mean familiarity with the picture stimuli was 2 *SDs* below that of all participants. Participants had spent at least two quarters on campus before participating.

Design The methodology of the study was both experimental and correlational. The experimental factors were picture heading (within subjects) and default heading (between subjects). The correlational factors are familiarity, SOD, and strategy use. Participants were randomly assigned to one of the four default headings (19 participants faced north, 18 east, 17 south, and 18 west) and completed forty-five trials, one for each picture.

Materials The experiment took place in a room that was aligned with the main axes of the campus (and the cardinal directions). The experimental room had one east-facing window that was open during the experiment. The view directly out that window was of a major pathway and a large (eight storey) building. However, if one stood next to the window, one could see the mountains and ocean (major orientation markers for the campus), and a few major buildings. Therefore, the window afforded excellent views for initial orientation to the campus (when standing near the window), but only basic information while participants completed the experiment.

Experimenters arranged a chair and laptop facing the assigned default heading before each participant arrived. The large table at which participants were seated (but in different orientations) was aligned with the room, the room was aligned with campus, and campus is aligned with the cardinal directions. Therefore, the space was aligned with respect to the default headings and response headings. This alignment was never mentioned to participants.

The photographic stimuli were sourced from the 36 most familiar photographs from a previous experiment (Burte & Hegarty, 2012), and nine new photographs (two north and seven east), for a total of 45 pictures. A global positioning device (GPS) was used to ensure that photographs were taken facing the cardinal directions. Photographs were taken of highly recognizable building facades and were cropped to exclude surrounding buildings or large-scale landmarks.

A typical trial started with viewing a photograph of campus on a computer, and participants responded by using a keypad with four arrows (front, right, back, and left). The participant determined the direction (with respect to the campus environment) in which the photographer stood to take the photograph (i.e., picture heading) and pressed a button to reproduce that direction. For example, if the photograph was taken facing south, and the participant was facing north, then the participant should press the downward arrow to indicate the direction behind him/her.

Procedure Participants were briefly introduced to the experiment, completed a demographics questionnaire, and then completed the Santa Barbara Sense of Direction (or SBSOD) scale (Hegarty et al., 2002). Next, participants

were asked to orient to the layout of campus while looking out the window. The experimenter asked the participant to point towards six major campus landmarks, to ensure that s/he was oriented to the global layout of the campus. The experimenter provided feedback, if needed, but most participants oriented and pointed correctly.

Participants were then introduced to the allocentric-heading recall task and presented with 12 practice trials in a fixed order. Participants were given feedback by being presented with the correct answer after each practice trial, and then completed 45 experimental trials without feedback.

After the allocentric-heading recall task, participants rated their familiarity with each photograph location on a 7-point Likert scale, with 1 being "Very familiar" and 7 being "Not at all familiar". As an objective measure of familiarity, participants were required to place an arrow on an unlabelled map of campus, to indicate the location and direction from which each photograph was taken. This map task and the familiarity task were used to ensure high familiarity with each photograph.

Finally, participants completed a strategy questionnaire that consisted of a free-response question, in which they entered the strategies they used, and then selected the strategies they used from a list of potential strategies. The list was created based on pre-testing and consisted of strategies such as "Using cardinal directions", "Using large-scale landmarks to determine orientation (mountains, ocean, Isla Vista, etc.)", and "Imagining travelling to the location".

Results

Photograph Familiarity To ensure that participants were sufficiently familiar with the pictures, pictures needed to pass three criteria to be included in the analysis: (1) mean familiarity for each picture could not be 2*SDs* lower than grand mean familiarity, (2) less than 25% of participants needed to rate their familiarity as "6" or "7 – Not at all familiar" for each picture; and, (3) at least 25% of participants needed to correctly identify the orientation and location of the picture, on the map task. Given these criteria, seven photographs were dropped from analysis, resulting in 9 north-facing, 9 east-facing, 10 south-facing, and 10 west-facing pictures. The familiarity grand mean for the 38 photographs was 2.2. Familiarity ranged from 1.0 to 3.7 across participants and from 1.2 to 3.9 across pictures.

Accuracy Heading disparity (angular difference between default and picture heading) served as the main independent measure. For example, if the picture heading was aligned with the default heading for a particular participant and trial, then this trial would be labeled as having a 0° heading disparity. A 4 (Heading disparity: 0°, 90°, 180°, 270°) by 2 (Gender) ANOVA comparing mean accuracy indicated a main effect of heading disparity, $F(3, 216) = 6.79$, $MSE = .13$, $p < .001$. The mean accuracy by heading disparity is shown in Figure 1. Post hoc tests revealed that the 180° condition was less accurate ($M = 54\%$) than all other conditions, which had similar accuracies (0° $M = 61\%$; 90°

$M = 64\%$; $270^\circ M = 63\%$). This can be interpreted as a detrimental effect on performance when one's body is positioned 180° away from the memory trace from one's head-direction cells when the location was last viewed. This detrimental effect is predicted by the animal-model hypothesis; however, we failed to replicate the predicted facilitation effect.

The main effect of gender was also significant, $F(1, 70) = 6.58$, $MSE = 1.32$, $p < .05$, with males being more accurate ($M = 67\%$) than females ($M = 54\%$). The interaction of heading disparity and gender was not significant, $F(3, 210) = 1.07$, $MSE = .02$, $p = .36$.

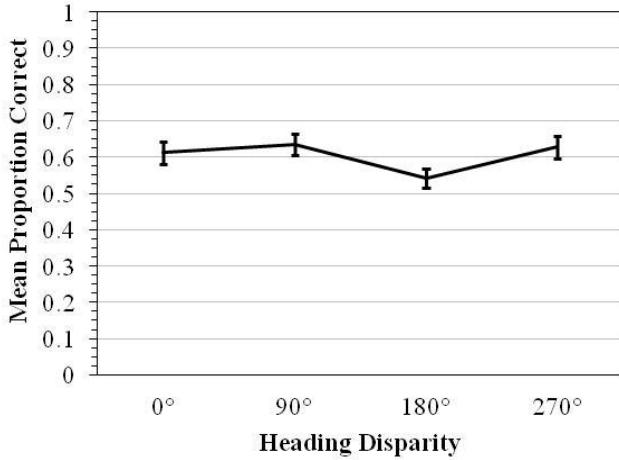


Figure 1: Mean accuracy rate as a function of heading disparity. Error bars are the standard errors of the mean.

Self-Reported Sense-of-Direction The correlation between SBSOD scores and overall accuracy was statistically significant, $r(70) = .31$, $p < .01$, indicating that people who rated themselves as having a good SOD were more accurate on the task. This correlation is similar to that found by Burte and Hegarty (2012); but substantially lower than those reported by Sholl et al. (2006). In addition, we failed to find a significant correlation between familiarity and SBSOD scores, $r(70) = .03$, $p = .81$, indicating that good SOD participants were not more accurate simply due to being more familiar with the photographs.

To further investigate individual differences in task performance, we compared the performance of good SOD (or GSOD) participants from the top 25% of the SBSOD distribution ($N = 18$), and poor SOD (or PSOD) from the bottom 25% ($N = 19$). A 2 (GSOD, PSOD) X 4 (Heading disparity: 0° , 90° , 180° , 270°) ANOVA comparing mean accuracy indicated significant main effects and a significant interaction. There was a main effect of heading disparity, $F(3, 105) = 3.60$, $MSE = .08$, $p < .05$, such that a heading disparity of 180° resulted in lower accuracy ($M = 54\%$) compared to 90° ($M = 63\%$) and 270° ($M = 64\%$). The heading disparity of 0° ($M = 60\%$) was not significantly different from other headings.

As shown in Figure 2, GSOD participants were significantly more accurate ($M = 71\%$) than PSOD

participants ($M = 49\%$), $F(1, 35) = 7.82$, $MSE = 1.78$, $p < .01$, and there was a significant interaction of SOD with heading disparity, $F(3, 105) = 2.60$, $MSE = .05$, $p < .05$. Importantly, the simple effect of heading disparity for GSOD participants was not significant, $F(3, 33) = 1.13$, $p = .35$, indicating that GSOD participants were equally accurate across all heading disparities. This is a novel finding and has not been found in previous studies (Sholl et al., 2006; Burte & Hegarty, 2012).

In contrast, the simple effect for PSOD participants indicated a significant difference across heading disparities, $F(3, 33) = 4.11$, $p < .05$. Not only are PSOD individuals less accurate on this task than GSOD participants, but they are significantly less accurate with 180° heading disparities compared to other disparities. This indicates that the detrimental effect of having one's body 180° misaligned with the picture, primarily affects PSOD individuals.

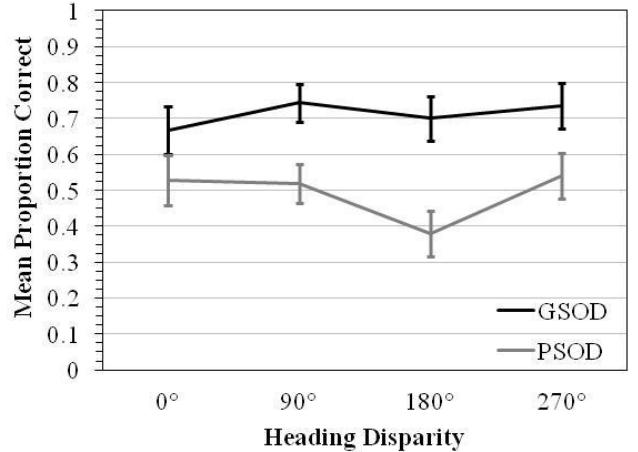


Figure 2: Mean accuracy rate as a function of heading disparity and SOD. Error bars are the standard errors of the mean.

Strategy Use To examine reported strategy differences, items in the strategy questionnaire were classified as egocentric or allocentric strategies (cf. Kozhevnikov & Hegarty, 2001). Example items from the egocentric strategy were “imagining myself standing at the photograph location”, “imagining traveling to the photograph location using campus walkways”, “comparing my current facing direction to the photographer’s facing direction at the photograph location”, etc. These strategies were labeled as ‘egocentric’ due to their reliance on thinking about directions in relationship to the participant’s body. Strategies that focused on thinking about directions in relationship to external frames of reference were labeled as ‘allocentric’. Examples of these items are “using a mental map or imaging a campus map”, “using cardinal directions”, “using large-scale landmarks”, etc.

Participants were classified into strategy groups by calculating z-scores to reflect each participant’s tendency to use each strategy compared to that of the entire group. For each participant, the egocentric and allocentric z-scores

were compared and if the two scores differed by more than $.75\text{ SDs}$, the participant was deemed to have used one strategy more than the other. If the z -scores did not differ by $.75\text{ SDs}$, the participant was classified as using a mixed strategy. This resulted in 33 participants who used a mixed strategy, 15 who used an egocentric strategy, and 24 who used an allocentric strategy.

Strategy Use and Sense-of-Direction To test the relationship between SOD and strategy, we compared the SBSOD scores of those classified as using egocentric and allocentric strategies. Egocentric strategy use corresponded with lower (or poorer) SBSOD scores ($M = 3.7$, $SEM = .2$) and allocentric strategy use corresponded with higher (or better) SBSOD scores ($M = 4.5$, $SEM = .2$), and this difference was statistically significant, $t(37) = -2.24$, $p < .05$.

Looking at strategy use across PSOD and GSOD individuals, we see that PSOD individuals used egocentric ($N = 8$), allocentric ($N = 6$), and mixed strategies ($N = 5$). However, GSOD individuals only reported using allocentric strategies ($N = 8$) and mixed strategies ($N = 10$). A chi-squared test revealed a significant relationship between SOD and strategy, $\chi^2(2, N = 37) = 9.93$, $p < .01$. GSOD individuals were less likely to use egocentric strategies than predicted by chance.

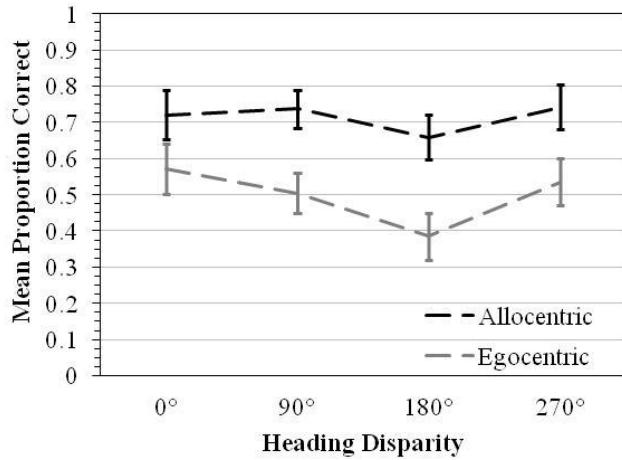


Figure 3: Mean accuracy rate as a function of heading disparity and strategy. Error bars are the standard errors of the mean.

Strategy Use and Accuracy A 2 (Strategy: egocentric or allocentric) \times 4 (Heading disparity: 0° , 90° , 180° , 270°) ANOVA indicated a significant main effect of heading disparity, $F(3, 111) = 6.07$, $MSE = .12$, $p < .001$, a significant main effect of strategy, $F(1, 37) = 9.50$, $MSE = 1.72$, $p < .01$, and a non-significant interaction, $F(3, 111) = 1.27$, $MSE = .03$, $p = .29$. Figure 3 shows the mean accuracy by heading disparity. Participants who tended to use allocentric strategies were significantly more accurate ($M = 72\%$) than those who tended to use egocentric strategies ($M = 50\%$). While Figure 3 shows a trend for allocentric strategy users to show a weaker alignment effect, this trend

was not statistically significant. The finding that strategy use impacts the accuracy with which participants respond to the allocentric-heading task is a novel finding and is not predicted by the animal-model hypothesis.

Photograph Familiarity and Accuracy Correlations between participants' mean familiarity rating (averaged over the 38 pictures) and their mean accuracy on the heading-recall task were not significant, $r(70) = .03$, $p = .81$. This indicates that participants, who rated their familiarity as high, were not more accurate than participants with lower familiarity. One interpretation is that all participants had a level of familiarity high enough, as to not hinder their task performance. However, correlating mean familiarity per picture (averaged over individuals) with mean accuracy per picture resulted in a significant correlation, $r(36) = -.49$, $p < .01$. This suggests that despite pretesting for familiarity, some familiarity differences remained between the pictures. Importantly, as default heading is manipulated between participants, differences in picture familiarity cannot account for the effects of heading disparity on performance.

Discussion

We replicated findings that individuals can recall allocentric-directional information from pictures, and that individual performance in the allocentric-heading recall task is related to SOD (Sholl et al., 2006; Burte & Hegarty, 2012). We also showed that these results replicate with a button-press response rather than the more body-based response of turning in one's chair. Importantly, we provided evidence for the use two strategies in this task, and showed that strategy use was related to self-reported SOD. GSOD participants reported using allocentric or mixed strategies, compared to PSOD participants were equally divided across strategy groups. Furthermore these groups had very different patterns of performance; PSOD individuals showed an alignment effect while GSOD did not. This pattern suggests that allocentric strategy use resulted in better performance, in general, and the alignment effect primarily affects PSOD individuals.

Changing the response mode, from turning in a chair to pressing a button, led to a weakened relationship between heading disparity and accuracy relative to previous studies. Specifically, the facilitation effect at 0° was not found. Another weakened relationship was the correlation of SOD with accuracy. Our correlations were noticeably lower than those found by Sholl et al (2006); therefore, this experiment adds doubt to the conclusion that that SOD solely reflects the operation of the human head-direction system. Instead, self-reported SOD might also relate to strategy differences.

Egocentric strategy use resulted in decreased accuracy in general and decreased accuracy for larger heading disparities (an alignment effect). Allocentric strategy use resulted in somewhat more equivalent accuracy across heading disparities. Although the interaction of strategy and heading disparity was not significant in the present study, the trends are notable in that they are similar to trends found

by Kozhevnikov et al. (2006) using JRD tasks.

Although we found both strategy differences and performance differences between those with good and poor sense-of-direction, the relationship between SOD, strategy, and performance remains ambiguous. Participants who used the egocentric strategy were more likely to have a lower (or poor) SOD, and those who used the allocentric strategy were more likely to have a higher (or good) SOD. Good SOD participants were also less likely to use egocentric strategies, than would be predicted by chance. But the causal relationships between strategy differences, individual differences and performance are currently unclear, as having a good SOD could cause people to use the allocentric strategy or repeated use of the allocentric strategy could contribute to having a good SOD. We are investigating the causal relationship between strategy use, SOD, and performance in a current study.

The newly discovered strategy differences between good SOD participants and poor SOD participants might have been due to the replacement of the body-based response with the button-press response. It is possible that the response of turning in one's chair in previous studies forced participants to use an egocentric strategy, which resulted in the alignment effect for participants of all ability levels. Perhaps, pressing a button did not force participants into using an egocentric strategy, so good SOD participants were freed from this restriction to think in terms of their body. This allowed good SOD participants to demonstrate similar performance across differing default headings. While our findings cannot provide support for these ideas, our findings do suggest that individual and strategy differences need to be incorporated into accounts of the performance within the allocentric-heading task. Research is also needed to determine if the response mode change was responsible for the identification of strategy differences.

We found a more nuanced relationship between familiarity and performance than in our earlier study (Burte & Hegarty, 2012). Specifically, familiarity was correlated with performance, but only when compared across pictures, and overall familiarity with the pictures was unrelated to SOD. It seems that our goal to use only familiar photographs was achieved, as accuracy was not correlated with mean familiarity for all pictures; however, the familiarity rating of individual photographs still impacted accuracy. Since recognition of a location is likely the first step in completing the allocentric-heading task, it follows that familiarity on a picture-by-picture basis would affect accuracy.

Another novel finding of this study is that we found gender differences in task performance. It is possible that females are more tied to their bodies than males, which leads to a greater gender difference with a button-press response than a more body-based response (i.e., turning). Future experiments should continue to monitor gender differences in this task.

In conclusion, we found novel evidence for strategy differences in the allocentric-heading recall task and these

differences are related to level of performance and self-reported sense-of-direction. Given similar findings in navigational tasks, we propose that choice of strategy is a critical element to the understanding of individual differences within spatial tasks. Specifically, this study demonstrates that individual and strategy differences can be found within tasks that are often conceptualized as universal or invariant cognitive processes. Neuroscientific research using animals has provided the foundation for understanding the functional architecture of human spatial abilities. Now, there is a need to incorporate the unique aspects of human cognition – like strategy and individual differences – into the functional architecture.

Acknowledgments

This research was supported by the Institute for Collaborative Biotechnologies.

References

Burte, H., & Hegarty, M. (2012). Revisiting the Relationship between Allocentric-Heading Recall and Self-Reported Sense of Direction. In N. Miyake, D. Peebles, & R. P. Cooper (Eds.), *Proceedings of the 34th Annual Conference of the Cognitive Science Society* (pp. 162-167). Austin, TX: Cognitive Science Society.

Hegarty, M., Richardson, A. E., Montello, D. R., Lovelace, K., & Subbiah, I. (2002). Development of a self-report measure of environmental spatial ability. *Intelligence*, 30, 425-447.

Ishikawa, T., & Montello, D. R. (2006). Spatial knowledge acquisition from direct experience in the environment: Individual differences in the development of metric knowledge and the integration of separately learned places. *Cognitive psychology*, 52(2), 93-129.

Kozhevnikov, M., & Hegarty, M. (2001). A dissociation between object manipulation spatial ability and spatial orientation ability. *Memory & Cognition*, 29(5), 745-756.

Kozhevnikov, M., Motes, M. A., Rasch, B., & Blajenkova, O. (2006). Perspective-taking vs. mental rotation transformations and how they predict spatial navigation performance. *Applied Cognitive Psychology*, 20(3), 397-417.

Kozlowski, L. T., & Bryant, K. J. (1977). Sense of direction, spatial orientation, and cognitive maps. *Journal of Experimental Psychology: Human Perception and Performance*, 3, 590-598.

Prestopnik, J. L., & Roskos-Ewoldsen, B. (2000). The relations among wayfinding strategy use, sense of direction, sex, familiarity, and wayfinding ability. *Journal of Environmental Psychology*, 20(2), 177-191.

Ranck, J. B., Jr. (1984). Head-direction cells in the deep cell layers of dorsal presubiculum in freely moving rats. *Society of Neuroscience Abstracts*, 10, 599.

Sholl, M. J., Kenny, R. J., & DellaPorta, K. A. (2006). Allocentric-heading recall and its relation to self-reported sense-of-direction. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 32(3), 516-533.