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Research Report

Knowing where we're heading — When nothing moves

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ABSTRACT

Past research indicates that observers rely strongly on flow-based and object-based motion information for determining egomotion or direction of heading. More recently, it has been shown that they also rely on displacement information that does not induce motion perception. As yet, little is known regarding the specific displacement cues that are used for heading estimation. In Experiment 1a, we show that the accuracy of heading estimates increases, as more displacement cues are available. In Experiments 1b and 2, we show that observers rely mostly on the displacement of objects and geometric cues for estimating heading. In Experiment 3, we show that the accuracy of detecting changes in heading when displacement cues are used is low. The results are interpreted in terms of two systems that may be available for estimating heading, one relying on movement information and providing navigational mechanisms, the other relying on displacement information and providing navigational planning and orienting mechanisms.

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1. Introduction

As we navigate through the world, we must simultaneously solve a number of tasks. One, we must continually plan where we want to move next. Two, we must try to avoid colliding with obstacles, both static and moving, that may be on our path. And three, we must check that we are following the planned path. Solving these tasks requires the accurate and efficient determination of our direction of self-movement (also referred to as egomotion or heading). Research over the last few decades has shown that we rely on a number of visual cues to achieve this goal.

Gibson (1950, 1966) was the first to show the importance of optic flow information for determining egomotion. As an observer moves forward, an expanding radial flow pattern is generated in the optical array, and heading can thus be recovered from the flow field through global pooling of motion information. This idea has found substantial neurophysiolog-

ical support (e.g., Allman et al., 1985; Duffy and Wurtz, 1991a,b; Frost and Nakayama, 1983) and it has been conceptualized in a number of theories (e.g., Longuet-Higgins and Prazdny, 1980; Rieger and Lawton, 1985; Heeger and Jepson, 1990, 1992; Hildreth, 1992; Koenderink and van Doorn, 1987; Perrone and Stone, 1994, 1998; Warren and Saunders, 1995; Duffy, 2004).

As an alternative to these flow-based explanations, Cutting and his colleagues have proposed an object-based explanation, which emphasizes reliance on the retinal movement of salient objects for determining egomotion (e.g., Cutting, 1986, 1996; Cutting et al., 1992, 1997, 1999; Vishton and Cutting, 1995; Wang and Cutting, 1999). More specifically, these studies showed that we rely on at least three sources of object-based motion information for determining heading: the displacement direction of the largest (or nearest) object; the inward motion of objects nearer or farther than the fixation object; and the outward deceleration of these objects (Cutting et al., 1999). They also showed that object-based movement cues

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provided stronger heading cues than field-based motion information.

These results suggested that the direction of heading is determined primarily, if not exclusively, using motion information provided by flow fields and by the movement of salient objects in the visual field. In contrast, a recent study by Hahn et al. (2003) suggested that displacement information - rather than motion information - may also play a role in determining heading. Their subjects viewed sequentially presented pairs of digitized real world scenes and were asked to judge whether the perceived direction of heading was left or right. In one condition, the two views were presented with an interstimulus interval (ISI) of 1000 ms, yet subjects were still able to determine the direction of heading. The long ISI ensured that the stimuli were not only outside the window of visibility of low-level motion mechanisms (Watson et al., 1986) but also outside the range of classical apparent motion (e.g., Wertheimer, as cited in Sekuler (1996)). This indicates that heading can be determined in the absence of any motion information, that is, based on displacement information alone.

These results raise the question of why the human visual system may be relying on two different systems for heading estimation, especially when one of them, the motion-based system, has been shown to be very efficient and accurate. One interpretation is motivated by Milner and Goodale's (1995) distinction between the perception and action pathways. In this framework, heading estimation based on motion information would be mediated by the processing in the dorsal pathway, which is concerned with the visual control of actions. Heading estimation based on displacement information would be mediated by processing in the ventral pathway, which is more concerned with action planning and selection (Goodale and Milner, 2004; Glover, 2004). A second interpretation is motivated by the literature on orienting and reorienting in navigation (Healy, 1998; Shettleworth, 1998; Hermer and Spelke, 1996; Kelly and Bischof, 2005, 2008). Animals, including humans, need to establish their orientation when they begin to navigate to a different location. During navigation, they need to re-orient whenever a discrepancy is detected between the internally updated sense of orientation and the external world. In this framework, heading estimation based on motion information would be provided by the navigational system, whereas heading estimation based on displacement information would be provided by the orienting and re-orienting system.

Taken together, the studies provide evidence that observers rely not only on motion information, but possibly also on displacement information for determining the direction of heading. Many questions remain open regarding the nature of the latter information source. For instance, are all available displacement cues or only subsets of those cues used for heading estimation? And if only subsets are used, which ones are preferentially used? Studies by Enriquez and colleagues provide partial answers. Specifically, observers use objects as landmarks to infer heading (Enriquez et al., 2003); in sparse scenes, they do not encode all objects for estimating heading (Enriquez et al., 2004); and they are capable of selectively attending to the objects in a scene that are important for estimating heading (Enriquez et al., 2005). The goal of the present study was to investigate the use of displacement

information in heading estimation by examining how it is affected by the nature and the number of displacement cues (Experiment 1a) and by the availability of near and far cues (Experiments 1b and 2). Finally, we investigated the ability to detect *changes* in heading direction from displacement cues (Experiment 3).

2. Experiment 1

The first experiment extended the basic paradigm of Hahn et al. (2003). In contrast to the natural scene (i.e., a hallway with doors, ceiling lights, and floor reflections in Experiment 1) used by Hahn et al., pairs of similar, computer-generated hallways scenes were used in the present study. As in Hahn et al. (2003), (i) two successive scenes, in which the observer moved horizontally to the left or right or forward and horizontally to the left or right, were presented with an ISI sufficiently long to eliminate apparent motion; (ii) eight horizontal displacements were used; and (iii) observers were asked to judge the perceived direction of heading (i.e., left or right) with a dichotomous key press. The Hahn et al. paradigm was also extended in several ways as described below.

In Experiment 1a, the number of available informational displacement cues was varied, with four graphically rendered scene types (see the upper panel of Fig. 1) to contain maximal cues (a hallway with doors, ceiling lights, and floor reflections) down to minimal cues (an empty hallway). If heading estimation using displacement cues is resolved by using many cues, then estimations should be least accurate when the number of cues is minimal (i.e., in the empty hallway scenes).

In Experiment 1b, the presence of near and far informational displacement cues was varied with three graphically rendered scene types that contained both near and far cues, only near cues, and only far cues (see upper panel of Fig. 2). If near objects are more important for determining heading than far objects, as is the case in dynamic settings, then estimations should be least accurate when near cues (i.e., doors) are absent. In addition, the initial image of the hallways was presented from five different viewpoints rather than a single, central starting position (as in Experiment 1a) to ensure that observers were basing their heading estimations on actual visual input rather than on a representation in memory.

2.1. Results

In this and all subsequent experiments, mean accuracies and RTs were determined as a function of scene type, movement direction, and horizontal displacement for each subject.

2.1.1. Accuracy data Experiment 1a

Accuracy was above the level of chance for each scene type [all t's>2.68, all p's<.05]. Mean accuracies for scene type and horizontal displacement are presented in the lower panel of Fig. 1. The data were analyzed with a 3-factor repeated measures analysis of variance (ANOVA) with scene type (scenes 1, 2, 3, 4), movement direction (left, right, forward and to the left, forward and to the right), and horizontal displacement (7.5, 15, 22.5, 30 cm) as factors. No statistically

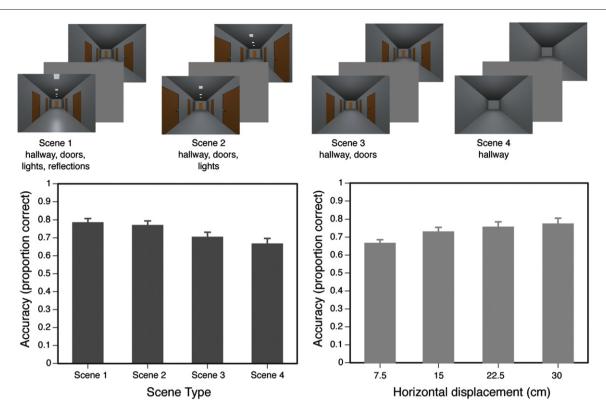


Fig. 1 – The upper panel illustrates the four synthetically generated scenes presented to subjects in Experiment 1a. From left to right: scene 1 containing a hallway with doors, ceiling lights, and a reflection from the lights on the floor; scene 2 containing a hallway with doors and ceiling lights; scene 3 containing a hallway with doors; and scene 4 containing an empty hallway only. For each scene, the temporal stimulus sequence is illustrated by the three pictures from bottom-left to top-right. The lower panel depicts accuracy data as a function of decreasing image information on the left and accuracy as a function of increasing horizontal magnitude displacements on the right.

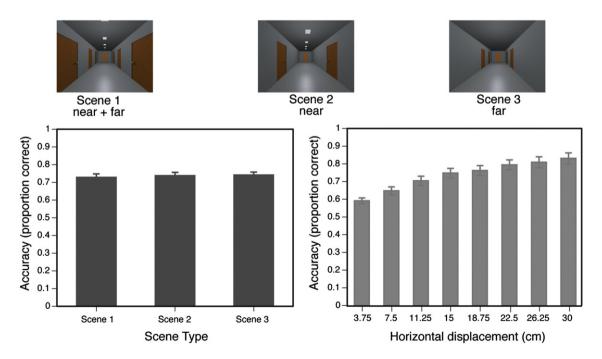


Fig. 2 – The upper panel illustrates the three scene types presented to subjects in Experiment 1b. Scene 1 contained both near and far information cues (i.e., front lights and doors and back lights and doors); scene 2 contained only near cues; and scene 3 contained only far cues. The lower panel depicts accuracy data as a function of decreasing image information on the left and accuracy as a function of increasing horizontal displacements on the right.

significant effects were observed for movement direction or any of its interactions [all F's<1]. Given that accuracy was not affected by movement direction, despite the large range of movement direction (5.7°–21.8° for left and right movements that involved a forward step and 90° for left and right movements that did not involve a forward step), we collapsed across this factor and conducted a 2-factor repeated measures ANOVA with scene type and horizontal displacement as factors.

Statistically significant effects were found for scene type and horizontal displacement [both F's>3.66, both p's<.05] (see the lower panel of Fig. 1). Separate linear contrasts of scene type and horizontal displacement indicated that accuracy decreased with the reduction of available informational cues in the scene and increased with larger displacements [both F's>10.49, both p's<.01]. The scene type×horizontal displacement interaction [F(9, 171)=1.57, p>.1] was not statistically significant, indicating that accuracy increased equally with larger displacements in all 4 scene types.

2.1.2. Reaction time data Experiment 1a

Average RT was $1142 \, \text{ms}$ (SE=158 ms). A 2-factor repeated measures ANOVA on mean correct RT with scene type and horizontal displacement as factors revealed a statistically significant main effect for horizontal displacement [F(3, 57) = 2.95, p < .05]. A linear contrast indicated faster RTs with larger displacements [F(1, 57)=8.13, p < .01]. No other statistically significant results were observed [both F's < 1.68, both p's > .1].

2.1.3. Accuracy data Experiment 1b

Accuracy was greater than chance levels for each of the 3 scene types [all t's>5.03, all p's<.001]. Mean accuracies for scene type and horizontal displacement are presented in the lower panel of Fig. 2. The data were analyzed using a 3-factor repeated measures ANOVA with scene type (scene 1, 2, 3), movement direction (forward and to the left, forward and to the right), and horizontal displacement (3.75, 7.5, 11.25, 15, 18.75, 22.5, 26.25, 30 cm) as factors. No statistically significant effect or interaction involving movement direction was found [all F's<1], hence a 2-factor repeated measures ANOVA was conducted with scene type and horizontal displacement as factors.

A statistically significant effect was not observed for scene type [F<1], indicating that both, near and far, cues were equally effective for determining heading (see the lower panel of Fig. 2). A statistically significant effect was observed for horizontal displacement [F(7,91)=19.07, p<.0001] with a linear contrast indicating that greater displacements increased accuracy of heading estimation [F(1, 91)=126.23, p<.0001]. The scene type×horizontal displacement interaction was not statistically significant [F<1].

2.1.4. Reaction time data Experiment 1b

Average RT was 1043 ms (SE=104 ms). A 2-factor ANOVA revealed neither a statistically significant effect nor an interaction for scene type [both F's<1]. A marginally statistically significant effect was observed for horizontal displacement [F(7, 91)=1.97, p.<.07], and a linear contrast indicated faster RTs with increases in horizontal displacement [F(1, 91)=6.09, p<.05].

2.2. Discussion

In Experiment 1a, we replicated Hahn et al.'s (2003) results by showing that accurate heading estimation could be obtained using displacement - rather than motion - cues. We also extended those findings by showing that accuracy in heading estimation decreased as the number of informational displacement cues decreased. Specifically, heading was judged most accurately for scene 1, which showed a hallway with doors, ceiling lights and reflections on the floor, and it was poorest for scene 4, which showed an empty hallway. The accuracy for scene 4 was, however, above chance level, indicating that heading estimation is not based exclusively on the perceived displacement of landmarks (i.e., objects), as suggested in past work (e.g., Enriquez et al., 2003, 2004). Rather, observers can also use other cues for estimating heading, including geometric cues provided by the environment.

Experiment 1b investigated whether near objects were more important than far objects for determining heading. At first glance, it appears that this is not the case, given that performance was the same whether near cues (scenes 1 and 2) or only far cues (scene 3) were available. However, a closer examination of the images reveals that even in scene 3, where the doors and lights are distant, observers may have been deriving near information from geometric cues (i.e., the ceiling/wall and the floor/wall corners). This interpretation is consistent with the results of Experiment 1a, which indicated that these cues may be used for estimating heading.

Experiment 1b also investigated whether observers obtained an estimate of their heading from the sequentially presented images or whether they were simply creating one mental representation of the initial image on which they based all subsequent heading judgments. The results showed that observers are able to determine heading from the displacement cues, even when the viewing position in the first image that they saw was varied randomly.

Finally, in both, Experiments 1a and 1b, greater accuracy and speed for heading estimation were obtained with larger horizontal displacements.

3. Experiment 2

Given that heading estimations were likely made using geometric environment cues in Experiment 1, our hypothesis that near objects may be more important than far objects for heading estimation remains to be tested. Importantly, there is an alternative hypothesis that must also be tested. That is, it is possible that near and far cues are not differentially weighted, as we hypothesized, but rather that the information for near

¹ Given that no differences were observed between the left and right movements and the forward and to the left and forward and to the right movements in Experiment 1a, we excluded the left and right movements with no forward movement from the remaining experiments.

and far objects is pooled. To this end, we generated virtual scenes containing a set of brightly patterned columns in an otherwise empty field, which lacked the near geometric information that had been available in the hallway scenes of Experiment 1. Specifically, four scene types were generated with the patterned columns in the (i) front, middle, and back field; (ii) front only; (iii) middle only; and (iv) back only (see the upper panel in Fig. 3).

3.1. Results

3.1.1. Accuracy data

Accuracy for each of the four scene types was above chance level [all t's>18.17, all p's<.0001], as was accuracy for each of the three horizontal displacements [all t's>6.76, all p's<.0001]. Mean accuracies for scene type and horizontal displacement are presented in the lower panel of Fig. 3. As in Experiment 1, data were analyzed using a 3-factor repeated measures ANOVA with scene type (scene 1, 2, 3, 4), movement direction (forward and to the left, forward and to the right), and horizontal displacement (7.5, 15, 22.5 cm; corresponding to heading angles of 14.0°, 26.6° and 36.9°, respectively) as factors. As in Experiments 1a and 1b, neither movement direction nor its interactions were statistically significant [all F's<1.99, all p's>.1] and thus the data were further analyzed using a 2-factor repeated measures ANOVA with scene type and horizontal displacement as factors.

A statistically significant effect was found for scene type [F(3, 45)=13.85, p<.0001] with a linear contrast indicating that

near objects were more effective for determining heading than far objects [F(1, 45)=40.55, p<.0001]. A statistically significant effect was observed for horizontal displacement [F(2, 45)=23.94, p<.0001] with a linear contrast indicating that larger displacements resulted in better performance [F(1, 45)=47.27, p<.0001]. A statistically significant scene type×horizontal displacement interaction was not observed [F<1], indicating that, in all scenes, accuracy increased equally with larger displacements.

3.1.2. Reaction time data

Average RT was 1456 ms (SE=220 ms). The 2-factor ANOVA on mean correct RTs did not reveal any statistically significant effects or an interaction [all F's<1.02, all p's>.3].

3.2. Discussion

This experiment was aimed at investigating the influence of near and far landmarks on the accuracy of heading estimation. Observers judged the heading direction in scenes containing many landmarks (i.e., columns) at various distances on a background that was devoid of other (i.e., near or far) reference cues. The results were clear: accuracy of heading estimation was significantly higher for scenes with near landmarks (i.e., scenes 1 and 2) than for scenes with intermediate or far landmarks (i.e., scenes 3 and 4). Hence, nearer objects are a more reliable source of information for determining heading than more distant objects are.

Alternatively, heading estimation could have been based on the pooled displacement information of all landmarks, as

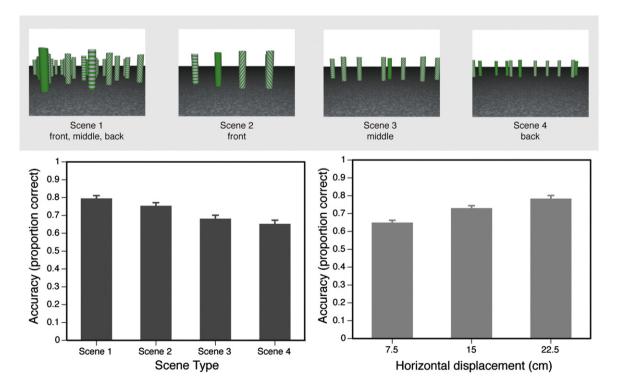


Fig. 3 – The upper panel illustrates the four scene types presented to subjects in Experiment 2. Scene 1 contained columns in the front, middle, and back sections, scene 2 contained columns only in the front section, scene 3 contained columns only in the middle section, and scene 4 contained columns only in the back section. The lower panel depicts accuracy data as a function of scene type is presented on the left and accuracy as a function of increasing horizontal displacements is presented on the right.

well as other available cues, as was the case in the hallway scenes of Experiments 1a and 1b. If this were so, then accuracy of heading estimation should be better for scene 1 than for scene 2 because the former contains many more landmarks. However, there was no difference in accuracy between scenes 1 and 2, indicating that observers were not simply pooling displacement information of all landmarks. Rather, they were relying more on the displacement of near landmarks.

Consistent with Experiments 1a and 1b, there was again a significant effect of horizontal displacement, with larger displacements (i.e., larger heading angles) vs. smaller displacements resulting in greater accuracy of heading estimation. If heading estimation was simply based on the average retinal displacement of all landmarks (i.e., objects), then one would expect a scene type by horizontal displacement interaction. The absence of an interaction further confirms that observers were using landmarks selectively for heading estimation.

Although accuracies in estimating heading were significantly above chance level, they were very low, even for large heading angles, indicating that heading estimation based on the displacement of landmarks (rather than their perceived motion) is not very accurate. This result stands in contrast to Vishton and Cutting (1995), who found much higher accuracies of heading estimation under somewhat similar conditions. More specifically, they found accuracies in the range of 84-87% for heading angles in the range of 2°-8° (with a somewhat lower density of landmarks, and with 3 frames presented at .42 frames/s; p. 989), whereas in our case the accuracy for the smallest heading angle of 14.0° was only 63%. These differences are too large to be explained by the moderate differences in landmark density or by the difference in number of frames (two in our case, three in Vishton and Cutting, 1995), even if one takes probability summation (Watson, 1978) into account. Two important differences between the stimuli may, however, account for these differences in results. First, Vishton and Cutting's (1995) stimuli consisted of line drawings of trees. Accordingly, the landmark trees could not be occluded by other objects, whereas in our case, near columns were likely to occlude columns that were farther away. Second, Vishton and Cutting singled out one special landmark, a red fixation tree, and encouraged observers to base their heading judgments with respect to that landmark. In contrast, we neither used a salient fixation landmark nor did we encourage observers to use a particular strategy for making heading judgments.2

In summary, Experiments 1a, 1b, and 2 provided clear evidence that observers are able to make coarse heading estimates with displacement, rather than motion, information using both landmarks in the environment and geometric cues provided by the environment. Experiment 2 also showed that near cues provide a more reliable source for heading estimation than far cues. Finally, the results indicated that accuracy of heading estimation is fairly low.

4. Experiment 3

In Experiments 1a, 1b, and 2, we established that observers are able to estimate the direction of heading using displacement information (i.e., the displacement of geometric cues, and of near and far objects). The accuracy of heading estimation is, however, fairly low, especially for small displacements. Thus, motion-based heading estimation is significantly better than displacement-based heading estimation. In addition to estimating simple (translation) motion trajectories, the motionbased heading estimation can also be used for more complex (curved) motion trajectories that include a rotational component (e.g., see Lee et al., 2006; Royden, 1997; Stone and Perrone, 1997). Experiment 3 was designed to investigate whether heading estimation based on displacement information also works for more complex trajectories. To this end, we investigated whether subjects are able to detect changes in heading over a sequence of three successive frames that defined two movement steps.

Specifically, the first movement step (i.e., between frame 1 and frame 2) was equally likely forward, forward and to the left, or forward and to the right. The second movement step (i.e., between frame 2 and frame 3) continued the trajectory established in the first movement step except that a horizontal shift either to the left or to the right was added. The upper panel of Fig. 4 gives an example of the sequence of events for each of the three types of first movements (i.e., forward, forward and to the left and forward and to the right). We hypothesized that the larger the trajectory difference between the first and second movement steps, the better observers would be at identifying the change in trajectory. The horizontal difference between the first and second movement steps for all experimental conditions and the corresponding angular differences of the trajectories are presented in Table 1. The middle panel of Fig. 4 illustrates all possible movement combinations. The observers' task was to indicate whether the second movement step (i.e., the trajectory established between frame 2 and frame 3) was to the left or to the right of the trajectory established in the first movement step (i.e., the trajectory established between frame 1 and frame 2).

4.1. Results

Accuracy of detecting changes in heading was analyzed with two separate ANOVAs to explore accelerations following: (i) an initial forward only movement; and (ii) an initial forward and to the left movement and an initial forward and to the right movement. Mean accuracies and mean correct RTs were determined. Mean accuracies for each of the 18 movement combinations are presented in the lower panel of Fig. 4 as a function of the initial movement step.

4.1.1. Accuracy data

4.1.1.1. Initial forward movement. A 2-factor ANOVA assessed effects of acceleration on accuracy with second movement direction (left, right) and horizontal displacement (15, 30, 45 cm) as factors. Both main effects and the interaction were statistically

² Additionally, in a pilot study we inserted a red "fixation column" in the centre of the image and asked observers to make heading judgments relative to this column. Accuracy levels increased substantially in this condition.

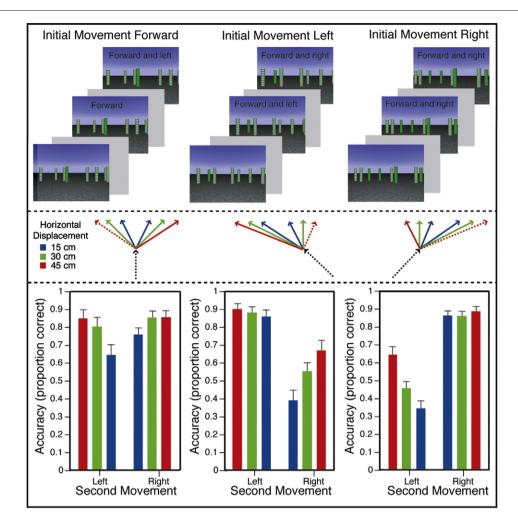


Fig. 4 – The upper panel illustrates an example of the temporal stimulus sequence (bottom-left to top-right) for each type of initial movement (i.e., forward only, forward and to the right, and forward and to the left) in Experiment 3. The middle panel illustrates a bird's eye view of all possible movement combinations, with the dotted lines depicting the movements shown for each of the initial movements illustrated in the upper panel. The lower panel illustrates accuracy as a function of the second movement steps (15, 30, and 45 cm left and right) for each type of initial movement.

significant [all F's>4.27, all p's<.05]. A linear contrast of horizontal displacement revealed increased accuracy with horizontal displacement [F(1, 33)=65.95, p<.0001]. In addition, contrasts of the interaction revealed that for the smallest displacement performance was better for a right than a left movement [F(1, 66)=18.69, p<.0001].

4.1.1.2. Initial left or right movement. A 3-factor ANOVA assessed acceleration effects on accuracy with initial movement (forward and to the left, forward and to the right), second movement direction (same — left then left, right then right or different — left then right, right then left), and horizontal displacement (15, 30, 45 cm) as factors. A statistically significant main effect of initial movement was observed [F(1, 33) = 6.15, p < .05] with better performance when the initial movement was left (Ms=.71 and .67 for left and right movements, respectively). Statistically significant main effects were also found for second movement direction and horizontal displacement and their interaction [all F's>31.86, all p's< .0001]. These findings indicate that accuracy was higher when the second movement continued in the same direction as the

initial movement (Ms=.87 and .51 for movements in the same and different directions, respectively) and that larger horizontal displacements yielded greater increases in accuracy only when the second movement continued in a different direction than the initial movement (e.g., left then right; see Table 1).

To investigate whether observers are able to detect changes in heading, we analyzed the accuracy of detecting heading changes between the initial and second movement (see Table 1). Accuracy ranged from .34 to .88 for a direction change of 18.4° (movement combinations 8, 10, 15, and 17) and from .45 to .85 for a direction change of 18.4° (movement combinations 2, 5, 11, and 14), indicating that accuracy was not simply determined by the magnitude of the direction changes. Rather, the data indicate that observers tended to base their estimate on the initial movement trajectory and reliably detected only very large changes in movement direction (i.e., 71.6° for movement combinations 12 and 13). This poor performance stands in contrast to the high accuracy of motion-based heading estimation in curved trajectories (Stone and Perrone, 1997; Li and Warren, 2004).

Table 1 – Movement combinations used in Experiment 3. The first movement trajectory (between frame 1 and frame 2) is shown in the second column, the second movement trajectory (between frame 2 and frame 3) is shown in the third column, the horizontal difference between the two trajectories is shown in the fourth column, and the angular difference between the two trajectories is shown in the fifth column.

Movement combination	First movement trajectory	Second movement trajectory	Horizontal difference of trajectories (cm)	Angular difference of trajectories (°)
1	30 cm forward	30 cm forward+45 cm to the left	-45	-56.3
2		30 cm forward+30 cm to the left	-30	-45
3		30 cm forward+15 cm to the left	–1 5	-26.6
4		30 cm forward+15 cm to the right	+15	+26.6
5		30 cm forward + 30 cm to the right	+30	+45
6		30 cm forward+45 cm to the right	+45	+56.3
7	30 cm forward + 30 cm left	30 cm forward+75 cm to the left	-45	-23.2
8		30 cm forward+60 cm to the left	-30	-18.4
9		30 cm forward+45 cm to the left	-15	-11.3
10		30 cm forward+15 cm to the left	+15	+18.4
11		30 cm forward	+30	+45
12		30 cm forward + 15 cm to the right	+45	+71.6
13	30 cm forward + 30 cm right	30 cm forward+15 cm to the left	-45	-71.6
14		30 cm forward	-30	-45
15		30 cm forward+15 cm to the right	-15	-18.4
16		30 cm forward+45 cm to the right	+15	+11.3
17		30 cm forward+60 cm to the right	+30	+18.4
18		30 cm forward+75 cm to the right	+45	+23.2

4.1.2. Reaction time data

4.1.2.1. Initial forward movement. Average RT was 1277 ms (SE=66 ms). A 2-factor ANOVA on mean correct RTs revealed a statistically significant effect of horizontal displacement [F(2, 6) = 15.45, p < .0001], with a linear contrast indicating that accuracy improved with horizontal displacement [F(1, 66) = 30.14, p < .0001].

4.1.2.2. Initial left or right movement. Average RT was 1348 ms (SE=61 ms). A 3-factor ANOVA on mean correct RTs revealed a statistically significant effect of second movement and 2-way interactions involving initial movement and horizontal displacement [all F's>3.50, all p's<.05]. These results suggested that RTs were faster when the second movement was in the same direction as the initial movement. RTs were also faster for larger horizontal displacements, but only when the second movement was in a different direction than the initial movement [F(1, 66)=3.50, p<.05].

4.2. Discussion

As previously stated, motion-based heading estimation can be used reliably for estimating complex (e.g., curved) motion trajectories. The goal of Experiment 3 was to determine whether heading estimation based on displacement cues alone also works for these more complex trajectories. The verdict is clear: only very large changes in heading direction (i.e., greater than 70°) were reliably detected by observers. The pattern of results also indicates that judgments of heading changes were strongly biased by the direction of the first movement. The results of this experiment thus reveal a clear limitation of heading estimation based on displacement information. It can only be used for estimating the heading direction of simple (translational) trajectories but not for

estimating more complex movement trajectories, including changes in heading direction. Taken together, the results indicate that displacement-based heading estimation cannot operate as a substitute for motion-based heading estimation.

In addition, the conditions for the initial movement forward and second movement forward and to the left or right trials (i.e., movement combinations 1–6 in Table 1), are very similar to the conditions for the scene 3 trials in Experiment 2. It is noteworthy that the accuracy results obtained in both experiments are similar despite a number of minor differences between the experiments (e.g., differences in image background and the difference in the number of movement steps), indicating that our results on the estimation of heading from displacement information are quite robust and reliable.

5. General discussion

The purpose of the present study was to assess what displacement information observers use to estimate heading direction in the absence of any motion cues. Our results confirm the previous finding that observers can estimate their heading direction based on displacement information alone (Hahn et al., 2003; Enriquez et al., 2003, 2004, 2005), albeit with lower accuracy. Previous research has strongly supported an object-based approach to heading estimation, for displacement-based heading estimation (Enriquez et al., 2003, 2004, 2005). In contrast, our study suggests that heading estimation is not exclusively object-based, but can rely also on other geometric cues provided by the environment. This conclusion is supported by Experiment 1a, where observers were able to estimate their heading, although not very reliably, in a hallway completely void of any objects or landmarks, thus demonstrating their reliance on geometric cues provided by

the corners of ceiling, walls and floors. Further supporting evidence comes from Experiment 1b, where observers were able to estimate heading despite the fact that both the placement and the number of objects (i.e., landmarks) in the scenes varied considerably.

The present study was also aimed at determining whether information from different objects (i.e., landmarks) was pooled uniformly into a heading estimate, or whether they were weighted differentially. Experiment 2 provided the clearest evidence for differential weighting. First, accuracy of heading estimation for scene 2 containing front columns was significantly better than for either scenes 3 or 4 with middle and back columns, respectively, indicating that the accuracy of heading estimation was best when near landmarks were available. And second, accuracy of heading estimation for scene 1 with front, middle, and back cues was the same as for scene 2 with front cues only, indicating that the availability of landmarks farther away did not significantly improve accuracy of heading estimation.

The non-uniform reliance on different landmarks and different cues is consistent with Enriquez et al.'s (2004) finding that the visual system does not encode all information in a sparse scene for estimating heading. It is also consistent with Enriquez et al.'s (2005) finding that subjects can selectively attend to specific objects or groups of objects that are relevant for heading judgments. There are several possible reasons why observers relied more heavily on near landmarks/cues for heading estimation. Firstly, for a given forward movement, near objects are displaced significantly more in the retinal image than objects that are farther away, which permits more reliable heading estimation, even in the absence of movement information. Secondly, as we navigate through an environment, we are more likely to attend to near objects than to far objects possibly because we are, in the immediate future, more likely to collide with the near objects (Graziano and Cooke, 2006). And thirdly, it has been pointed out that for motion-based mechanisms, the displacement of the largest object provides a good heuristic for determining heading direction, and thus it is plausible that the same heuristic may also be used for displacement-based heading estimation (Cutting, 1996; Cutting et al., 1999).

The results of Experiments 1a, 1b, and 2 showed that accuracy of displacement-based heading estimation is fairly poor, operating only for large heading angles, and that it is substantially poorer than heading estimation from motion cues (e.g., Cutting et al., 1999; Vishton and Cutting, 1995; Warren and Saunders, 1995). In addition, the results of Experiment 3 indicated that displacement-based heading estimation is not used for estimating complex path trajectories, including curved ones. Thus, it is clear that displacement-based heading estimation cannot be seen as an alternative to motion-based heading estimation. Rather, as indicated earlier, it should be thought of as an additional mechanism for heading estimation that plays a number of roles, as discussed below.

There is neurophysiological evidence in support of the view that these two sources of information may be processed by two different subsystems — the dorsal and the ventral pathways. The dorsal pathway has been implicated as the neural substrate underlying the ability to judge heading based on motion information. Specifically, neurophysiological studies in animals

and humans have shown that the middle superior temporal area (MST) and its human equivalent (i.e., hMT/V5+) are recruited when subjects are asked to indicate their direction of heading (e.g., Britten and van Wezel, 1998, 2002; Peuskens et al., 2001; Vaina and Soloviev, 2004). The role of the dorsal stream in processing information necessary for egomotion is further supported by studies of patients with Alzheimer's disease (AD), some of whom show an impairment in optic flow perception, which may be related to their wayfinding deficit (Duffy et al., 2001). In addition, magnocellular-pathway deficits in patients with AD have been reported both psychophysically and electrophysiologically (Hache and Pasquier, 2002). And lastly, support for dorsal impairment comes from the demonstration of reduced blood flow in the left parietal-temporal lobe that may be associated with the wandering behavior observed in patients with AD (Rolland et al., 2005).

There is also neurological literature supporting ventral pathway involvement in heading estimation. If the dorsal pathway provided the only source of information for determining heading, then disruption of the dorsal pathway would result in an inability to determine heading. However, an investigation of patients with a damaged dorsal pathway, from traumatic brain injury or degenerative disease (e.g., AD), revealed that they were still able to navigate through the environment, albeit with greater difficulty (Gilmore et al., 1994). This finding suggests that navigation and heading information must also come from a source other than the dorsal pathway. The recovery of displacement information from scenes suggests that the ventral pathway may also be involved in determining and guiding heading.

Our dual system interpretation of heading estimation is also consistent with the literature on orienting and reorienting in navigation. Animals, including humans, need to establish their orientation when they begin to navigate to a different location, and during navigation they need to reorient whenever a discrepancy is detected between the internally updated sense of orientation and the external world (Healy, 1998; Shettleworth, 1998; Hermer and Spelke, 1996; Kelly and Bischof, 2005, 2008). In this framework, heading estimation based on motion information would be provided by the navigational mechanisms, whereas heading estimation based on displacement information would be provided by the orienting and re-orienting mechanisms.

In sum, our results suggest that heading estimation is provided by two systems. One is the dorsal pathway, which provides navigational mechanisms based on movement information. And the second is the ventral pathway, which provides navigational planning and orienting/re-orienting mechanisms based on visual displacement information. Our study has provided further insights into the mechanisms underlying orienting and navigational planning.

6. Experimental procedures

6.1. Experiment 1

6.1.1. Subjects

Twenty (9 males; mean age=22.3 years) and 14 (6 females; mean age=24.0 years) undergraduate students participated in

Experiments 1a and 1b, respectively. In all experiments reported here, all observers reported normal or corrected-to-normal vision and all gave written informed consent before the experiment and were given course credit or were paid for their participation.

6.1.2. Stimuli

POV-Ray (2002) was used to create the stimuli, which consisted of synthetically generated "hallway scenes" that were presented on a 32.4 by 24.5 cm colour monitor, corresponding to a visual angle of 35.9° by 27.5° at the viewing distance of 50 cm. The stimuli in Experiment 1a (see the upper panel of Fig. 1) consisted of the following scenes: a hallway with doors, ceiling lights, and a reflection from the lights on the floor (scene 1), a hallway with doors and ceiling lights (scene 2), a hallway with doors (scene 3), and an empty hallway (scene 4). The first frame was taken from a position in the centre of the hallway. For the second frame, the camera was moved relative to the starting position, with movement direction to the left, to the right, forward and to the left, and forward and to the right. Assuming a hallway width of 3 m, forward movements were approximately 75 cm and sideway movements (i.e., horizontal displacements) were 7.5, 15, 22.5 or 30 cm to the left or right. Hence there were 16 different movements for each scene type.

The stimuli in Experiment 1b were as in Experiment 1a, with the following exceptions. As depicted in the upper panel of Fig. 2, three hallway scenes were used, with lights and doors at the: front and back (i.e., near and far cues — scene 1); front only (i.e., near cues — scene 2); and back only (i.e., far cues scene 3). Movement directions were forward and to the left and forward and to the right. Again assuming a hallway width of 3 m, all movements were approximately 75 cm forward with horizontal displacements of 3.75, 7.5, 11.25, 15, 18.75, 22.5, 26.25, and 30 cm to the left and right, corresponding to heading angles of 2.9°, 5.7°, 8.5°, 11.2°, 14.0°, 16.7°, and 21.8°, respectively. In addition, 5 different viewpoints were generated for the initial frame — from the centre of the hallway, 15 cm to the left and right of centre, and 22.5 to the left and right of centre. Accuracy and reaction time (RT) were recorded by a computer.

6.1.3. Procedure

Observers were seated with their chins resting on a chin rest to prevent head movements. In each trial, frame 1 was shown for 500 ms, a blank screen followed for 1000 ms, and then frame 2 was shown for 500 ms. The observers' task was to indicate with a key press whether they were headed to the left (i.e., using the left arrow key) or to the right (i.e., using the right arrow key) relative to the frame 1. If they were headed to the left, they pressed. At the start of Experiment 1a, each observer received practice trials with scene 1 only. Practice blocks were repeated until the observer was correct on at least 80% of the trials in a single block up to a maximum of 10 blocks with a total of 160 trials.³ (All subjects learned the task in 10 or less blocks.) At the start of Experiment 1b, observers received practice trials with scene 1 only, with the initial frame

randomly chosen from any of the 5 different viewpoints, and horizontal displacements of 7.5, 15, 22.5, and 30 cm. In these and all subsequent experiments, on practice trials only, observers received feedback in the form of a 200 ms tone following an incorrect response.

In Experiment 1a, there were 24 blocks of experimental trials with a total of 384 trials. Of these 384 trials, there were 6 blocks of 16 trials for each of the 4 scene types (i.e., 96 trials/ scene type). Across the experiment, there were 16 trials for each scene type (4 movement directions: left, right, forward and to the left, and forward and to the right combined with 4 horizontal displacements: 7.5, 15, 22.5, and 30 cm). In Experiment 1b, there were 9 blocks of experimental trials with a total of 720 trials. Of these 720 trials, there were 3 blocks of 80 trials for each of the 3 scene types. Across the 240 trials/scene type, there were 8 horizontal displacements (3.75, 7.5, 11.25, 15, 18.75, 22.5, 26.25, and 30 cm) for each of the 2 movement directions (forward and to the left and forward and to the right) and from each of the 5 initial viewpoints (centre, 15 cm to the left and right of centre and 22.5 cm to the left and right of centre). The blocks of trials were presented in random order with the constraint that the same scene type could not occur in successive blocks.

6.2. Experiment 2

6.2.1. Subjects

Sixteen⁴ undergraduate students (7 males; mean age = 26.3 years) participated in this study.

6.2.2. Stimuli

As illustrated in the upper panel of Fig. 3, the stimuli consisted of 4 scene types containing columns on a textured field. To generate these scenes, the textured field was divided into 3 sections (i.e., front, middle, and back). Scene 1 contained a total of 24 columns with 5 columns in the front section, 8 columns in the middle section, and 11 columns in the back section. Scene 2 contained 5 columns in the front section, scene 3 contained 8 columns in the middle section, and scene 4 contained 11 columns in the back section.5 Assuming a column width of 30 cm, the column height was 75 cm, and the minimum distance between columns was 15 cm. Twenty initial frames were generated for each of the 4 scene types. From each initial frame, 6 additional frames were generated for use as frame 2 with the initial viewpoint displaced 30 cm forward and 7.5, 15, and 22.5 cm to the left and right (again assuming a column width of 30 cm), corresponding to heading angles of 14.0°, 26.6°, and 36.9°. With the exception of the practice block, all scene types appeared in random order in each block of trials.

6.2.3. Procedure

This was the same as in Experiment 1, with the following exceptions. There were 10 blocks of experimental trials with a

 $^{^{}m 3}$ This procedure for practice trials was observed in all subsequent experiments.

⁴ An additional subject was unable to meet the 80% accuracy criterion in the practice blocks and thus did not participate in the experimental blocks.

⁵ The number of columns in each section was chosen such that the average column density per unit area was approximately the same in each section.

total of 240 trials. In each block of 24 trials, there were with 6 trials for each of the 4 scene types (i.e., 1 trial per each of the 3 left and right displacements). For each of the 6 trials/scene within a block, one of the 20 available initial frames and its specified displacement was randomly selected.

6.3. Experiment 3

6.3.1. Subjects

Thirty-four undergraduate students (11 males; mean age=21.1 years) participated in this study.

6.3.2. Stimuli

The stimuli were similar to those used in Experiment 2 with the following exceptions. Only scene 3 images (i.e., middle columns) were presented and 3, rather than 2, frames were presented in succession, which defined two movement steps. In the first movement (i.e., from frame 1 to frame 2), the movement trajectory was equally likely to be forward, forward and to the left, or forward and to the right. In the second movement (i.e., from frame 2 to frame 3), the movement trajectory changed relative to the initial movement step and was equally likely to be to the left or to the right of the trajectory established in the initial step. The scene background was also different with a graduated blue, rather than white, sky and a dark grey, rather than light grey textured foreground.

6.3.3. Procedure

This was the same as in Experiment 2, with the following exceptions. Frame 2 was generated from each of the 20 initial frames by moving the observer along one of the following trajectories: 30 cm forward, or 30 cm forward and 30 cm left, or 30 cm forward and 30 cm right. Frame 3 was generated from frame 2 by moving the observer along the same trajectory as in the initial movement step plus an additional horizontal displacement of 15 cm, 30 cm, or 45 cm to the left or to the right (see Table 1). Following the presentation of frame 3, observers' indicated with a key press whether they were headed to the left or to the right relative to the trajectory established between frame 1 and frame 2. Subjects received 12 trials for each of the 18 movement combinations generated as described above for a total of 216 trials, which were randomly distributed into 6 blocks of 36 trials.

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