Heading perception from optic flow in the presence of biological motion

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We investigated whether biological motion biases heading estimation from optic flow in a similar manner to nonbiological moving objects. In two experiments, observers judged their heading from displays depicting linear translation over a random-dot ground with normal point light walkers, spatially scrambled point light walkers, or laterally moving objects composed of random dots. In Experiment 1, we found that both types of walkers biased heading estimates similarly to moving objects when they obscured the focus of expansion of the background flow. In Experiment 2, we also found that walkers biased heading estimates when they did not obscure the focus of expansion. These results show that both regular and scrambled biological motion affect heading estimation in a similar manner to simple moving objects, and suggest that biological motion is not preferentially processed for the perception of self-motion.

Introduction

Optic flow is defined as the pattern of retinal motion of elements in the environment generated when one moves through the environment (Gibson, 1950). It provides information about the direction of one's heading (Bruss & Horn, 1983; Longuet-Higgins & Prazdny, 1980). For linear translation without eye, head, or other extraneous movements, this analysis is relatively straightforward. In this case, the point in the optic flow pattern from which all motion vectors appear to originate, commonly termed the focus of expansion (FOE), corresponds to the direction in which one is heading. Studies have shown that in rigid environments, humans can detect their heading from optic flow to a level of accuracy adequate for safe locomotion (Cutting, Springer, Braren, & Johnson, 1992; Warren, Morris, & Kalish, 1988). Even when eye movements complicate the optic flow pattern by introducing rotational components to the flow field and thus dissociating the FOE from the heading direction, the direction of self-motion can still be accurately determined given extraretinal information about eye movements, or sufficient optic flow information (Li & Warren, 2000; Royden, Crowell, & Banks, 1994; Warren & Hannon, 1990).

Heading estimation from optic flow is fairly robust to perturbations of the visual field, such as the bounce and sway produced by walking (Cutting & Readinger, 2002; Kim, Growney, & Turvey, 1996), or the addition of random noise to the motion vectors in the flow field (van den Berg, 1992). This robustness is achieved by pooling motion vectors over large portions of the visual field, thus averaging out spurious motion while maintaining the global structure of the optic flow field required for heading estimation (Andersen & Saidpour, 2002; Lappe & Rauschecker, 1993; Perrone & Stone, 1994; Warren, Blackwell, Kurtz, Hatsopoulos, & Kalish, 1991).

Given the apparent robustness of heading detection mechanisms, it is somewhat surprising that one of the most common sources of noise in the visual environment, the motion generated by an object moving independently to the observer, has been shown to bias heading estimates by up to several degrees of visual angle (Layton & Fajen, 2015, 2016b; Li, Ni, Lappe, Niehorster, & Sun, 2018;

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Royden & Hildreth, 1996; Warren & Saunders, 1995). The direction of this heading bias is determined by the object's motion in depth relative to the observer. Laterally moving objects that also approach the observer in depth generate a bias in the direction opposite to object's lateral motion (Li et al., 2018; Warren & Saunders, 1995), whereas laterally moving objects that remain at a fixed distance from the observer generate a bias in same direction as object's lateral motion (Li et al., 2018; Royden & Hildreth, 1996).

Warren and Saunders (1995) proposed that a center-weighted spatial pooling hypothesis could account for the bias observed when translating toward a moving object. However, Royden and Hildreth (1996) contended that spatial pooling could not account for their finding that heading bias was in the opposite direction of an object's lateral motion when the object moved only laterally but not in depth. Consequently, Royden (2002; Royden & Hildreth, 1996) proposed that the differential motion between the object and the background could be used to explain their observed heading biases. This explanation is somewhat problematic though, as neurons responsive to differential motion do not project to the dorsal part of the medial superior temporal (MSTd) area, a key area responsible for heading estimation (Eifuku & Wurtz, 1998; Morrone et al., 2000; Nelissen, Vanduffel, & Orban, 2006). Layton and Fajen (2016b) have thus proposed that heading bias produced by object motion may arise from the discrepant optic flow generated within the object and the pseudo-FOE produced at the object's trailing edge. Layton et al. have modeled the bias as a peak shift produced by competitive interactions between neural representations of heading in MSTd (Layton & Fajen, 2016a; Layton, Mingolla, & Browning, 2012).

The above accounts are based on early studies that found a bias only when the moving object obscured the FOE of the background optic flow (Royden & Hildreth, 1996; Warren & Saunders, 1995). More recent studies found that moving objects can produce a heading bias when they are in close proximity, but do not obscure the FOE (Layton & Fajen, 2015). Li et al. (2018) showed that a laterally moving object can also induce a bias in heading judgments if the speed of the moving object is comparable to the speed of the background flow. They proposed a simple explanation based on the simulations of a long-standing model of heading perception (Lappe & Rauschecker, 1993). The model pools motion over the entire flow field without any segmentation or special processing of the moving objects and estimates the most-likely heading based on a full account of observer self-motion, i.e., both translation and rotation of the eye. Although the Warren and Saunders' model (1995) also pools motion over the entire flow field, it estimates heading by locating the FOE in the flow field instead of carrying out a full analysis of eye translation and rotation. Thus, unlike the Warren and Saunders' model, this model can account for both the bias in the opposite direction of object motion for objects approaching the observer on an oblique path (Li et al., 2018; Warren & Saunders, 1995) and the bias in the direction of object motion for laterally moving objects that remain at a fixed distance from the observer (Li et al., 2018; Royden & Hildreth, 1996). According to model simulations, the latter case is accounted for by a rotational component of observer/eye motion in addition to the translational component. Consequently, Li et al. (2018) concluded that heading biases reflect a pooling of the entire flow, a full analysis of self-motion components, and a lack of accounting for the moving object.

The aforementioned modeling and behavioral studies have only considered heading perception in the presence of abstract moving objects, predominantly rectangles or squares. In naturalistic settings, objects are often more complex. Other humans are one of the most common and behaviorally relevant examples of a complex moving object encountered frequently in the environment. When moving through scenes containing other people, an observer must consider their own forwards translation, the translation of the other actor, and the articulated pattern of biological motion generated by the actor's limbs. Limb motion introduces noise into the visual field, which can reduce the accuracy of heading estimation in the presence of moving people (e.g., Riddell & Lappe, 2018).

Though limb articulation may complicate heading estimation, the pattern of biological motion generated by people in the environment provides cues as to the nature of a walker's motion in the environment (Masselink & Lappe, 2015; Thurman & Lu, 2016). Theoretically, these cues could be used to facilitate the processing of walker motion, thus decreasing its influence on heading estimation.

The visual system is highly sensitive to biological motion and a variety of human actions can be readily recognized, even when they are only depicted by several points of light attached to the major joints of an actor (Johansson, 1973). Despite the highly degraded nature of these point light walkers (PLWs), observers can ascertain an abundance of information from their movements, including gender (Kozlowski & Cutting, 1977), emotion (Atkinson, Dittrich, Gemmell, & Young, 2004; Dittrich, Troscianko, Lea, & Morgan, 1996), and even a person's identity (Cutting & Kozlowski, 1977; Loula, Prasad, Harber, & Shiffrar, 2005). Importantly, biological motion can also be used to predict a person's actions and intentions (Blakemore & Decety, 2001; Diaz, Fajen, & Phillips, 2012; Graf et al., 2007) and provides signals as to the direction in which a person is moving (Beintema & Lappe, 2002; Lange, Georg, & Lappe, 2006; Mather, Radford, &

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West, 1992; Thornton, Pinto, & Shiffrar, 1998; Troje & Aust, 2013; Troje & Westhoff, 2006). During locomotion, such information must be processed in conjunction with optic flow and could either interfere with self-motion processing, or be integrated to provide more accurate estimates of object motion in the environment.

Cutting, Vishton, and Braren (1995) investigated the role of object familiarity on heading perception and found that, unlike simple objects, a walking human figure crossing the FOE did not bias heading estimation. This suggests that biological motion cues may also have been used to segment moving human figures before heading estimation. A dissociation of heading perception from biological motion perception was also described by Mayer, Riddell, and Lappe (2019), who investigated dual-task performance for heading and biological motion and found no interference. In contrast, Riddell and Lappe (2017) found that observers could dissociate self-motion from walker motion in ambiguous scenes, but estimated heading based on the optic flow produced by the combination of walker and ego-motion. This implies that heading perception simply pools all motion information and does not specifically account for biological motion information. Riddell and Lappe (2018) investigated heading perception when navigating through a crowd of walkers and reached a similar conclusion: PLWs contain valid cues for ego-motion estimation, but these can be extracted simply by pooling all motion information from the flow field. Given the high behavioral relevance of biological motion stimuli, the ability to perceive heading in the presence of biological motion warrants further investigation.

In the following experiments we tested the accuracy of heading perception in various situations containing normal PLWs, spatially scrambled PLWs, and laterally moving objects composed of random dots. Based on the prior studies above, which showed that heading perception is insensitive to object motion (Li et al., 2018) and to biological motion (Riddell & Lappe, 2017, 2018), we expected that biological motion is treated the same as rigid object motion with equivalent dimensions and mean velocity. Alternatively, given that biological motion provides information about human movement, it could be used to segment human motion from the scene to enable accurate heading estimation. If this is the case, biases should be smaller for scenes containing normal PLWs as compared to scenes populated by scrambled PLWs or moving objects.

Experiment 1: Heading biases produced by PLWs

The aim of Experiment 1 was to investigate whether both normal and scrambled PLWs bias heading estimation in a similar manner to a laterally moving object composed of random dots with no additional moving components, such as limbs. We placed normal PLWs, scrambled PLWs, and laterally moving objects on a ground plane and simulated observer translation through this environment. Observers were required to estimate their direction of heading at the end of a trial.

Despite their highly degraded nature, normal PLWs can be readily recognized as humans and easily discriminated from random motion (Bertenthal & Pinto, 1994; Cutting, Moore, & Morrison, 1988; Johansson, 1973). However, if the spatial relationships between the points are scrambled by randomizing the starting positions of each dot, recognition performance diminishes (Bertenthal & Pinto, 1994; Proffitt, Bertenthal, & Roberts, 1984). This scrambling process degrades walker recognition by removing any meaningful biological form, an essential characteristic of biological motion recognition (Beintema & Lappe, 2002; Lange & Lappe, 2006), but retains the same local trajectories as those present in an unscrambled walker (Cutting et al., 1988). Comparing heading performance in the presence of both normal PLWs and scrambled PLWs allows us to assess the influence of biological and complex, nonbiological motion on heading detection without modifying the total amount of motion signals in the scene. Comparing walker stimuli against laterally moving objects composed of random dots with no additional moving components allows us to assess whether the additional point motion generated by limb movement affects heading perception.

Biological motion processing depends on the duration of the stimulus (e.g., Lange & Lappe, 2006; Theusner, de Lussanet, & Lappe, 2014) and can be processed within 200–250 ms (e.g., Lange & Lappe, 2006; Theusner et al., 2014). If biological motion is used to segment human motion from the scene to enable accurate heading perception, at short trial durations (<200 ms), walkers might have a greater impact on heading estimation due to the fact that biological motion information is unavailable. At durations that are sufficient for biological motion perception (200–500 ms), heading perception might benefit from the biological motion cues. As such, we also manipulated trial durations to investigate whether stimulus duration played a role in this task.

We hypothesized that if biological motion cues facilitate the segmentation of human motion before heading estimation, the normal walker condition should produce smaller heading biases than the scrambled walker condition and the moving object condition. We also hypothesized that this effect may be modulated by the duration of the stimulus. Namely, differences between normal PLWs and the other conditions should only become apparent for durations larger than 200–250 ms.

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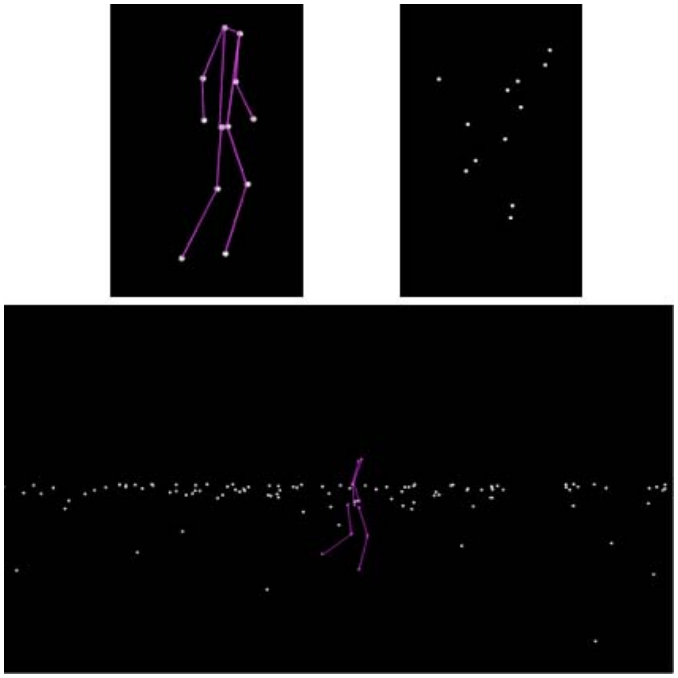

Figure 1. (A) Illustration of a normal PLW. (B) Illustration of the scrambled PLW and the moving object. For the scrambled walker, each point corresponds to one of the points of the normal walker and moves in the same manner as in the normal walker, but the starting positions of the points are randomly positioned. For the moving object, points were randomly positioned in the same manner but did not move with the articulation of the walker. (C) Illustration of the normal walker condition in Experiment 1. The joints of the walkers in (A) and (C) are highlighted in purple and connected by lines to assist the reader in recognizing their underlying human form. In the experiment, the lines were not visible and the walker points were colored white, same as the dots on the ground.

Methods

Observers

Nineteen observers took part in Experiment 1 (12 female, seven male, age: 19–28 years). One of these observers was an author and another observer was a research assistant. Aside from these two subjects, all observers were naive to the aims of this experiment. All observers had normal or corrected-to-normal binocular vision and gave written informed consent. Observers were compensated for their participation with either course credit or a small monetary payment. Ethical approval for the testing of all participants reported in the current study was obtained from the ethics board of the Department of Psychology and Sport Science of the Westfälische Wilhelms Universität, Münster, Germany. Sample sizes for the experiments reported here were decided based on similar previous research.

Materials

Stimuli for all three experiments were generated on an Apple MacBook Pro equipped with a 512 MB Intel HD Graphics 4000 on-board graphics card. A VDC Display Systems Marquee 8500 projector, projecting onto a 250 × 200 cm backlit screen was used to present the stimuli. The projector operated at a resolution of 800 × 600 pixels with a refresh rate of 60 Hz. Stimuli were programmed using MATLAB 2015b (MathWorks, Natick, MA) with the Psychophysics Toolbox (Version 3) add-on (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). Responses were signaled using a two-button mouse fitted with a tracking ball.

PLW generation

All walkers were derived from motion tracking data of a walking male, as seen from the profile view. The average walking speed of the actor was 1.4 m/s, with a single step cycle taking 1.24 s. Translational motion was not removed from the walkers such that they appeared to walk naturally across the scene. The walkers themselves consisted of 12 white points corresponding to the left and right ankle, knee, hip, hand, elbow, and shoulder joints. Each point subtended 1.14° of visual angle. At its largest possible size, an entire walker subtended 10.28° (width) × 18.18° (height).

Scrambled walkers were generated by randomizing the starting positions of each walker point, while retaining the points' individual trajectories. This scrambling process served to remove any meaningful biological form, though retained some relatedness between the points, as well as the same local motions as those present in an unscrambled walker. Example normal PLWs and scrambled PLWs can be seen in Figure 1.

A laterally moving object composed of random dots with no internal motion was used as a second control stimulus. This object consisted of 12 points that were randomly distributed over a rectangular area the same size of a walker. The object translated across the scene at the same speed of the walker, but the individual points did not move relative to each other. Objects and walkers translated laterally with respect to the observer.

Ground plane

The ground plane consisted of 1,000 white points randomly distributed over a 34 (width) × 100 m (depth) rectangular area, resulting in a dot density of 0.3 dots/m^2. The ground plane was located 1.4 m below the observer's eye height. The dots comprising the ground plane and those comprising the PLWs were equal in size and matched for luminance.

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Visual displays

The display (102.68° V × 90° H) simulated linear translation across the ground plane toward a random heading location. Three experimental and one control display conditions were tested: a normal walker condition, a scrambled walker condition, a laterally moving object condition, and a condition that presented only the background flow field with no other moving object. In all display conditions, translation across the ground plane was simulated by moving a virtual "camera" through the scene at 3 m/s. The camera's viewing direction was aligned with the z-axis of the virtual world. The heading location was determined by selecting a random position on the horizon of up to 15° to the left or right of the center of the display. In the three experimental conditions, the walker or the object was placed on the ground plane at a depth of 7 m, and up to 1.11 m to the left or right of the heading. The walker or the object moved on a perpendicular path to the observer (path angle of 90°) at a constant speed (1 m/s) towards the heading. They were positioned such that they would always obscure the FOE at some point during the course of a trial (Figure 1C).

Procedure

Trials began with a short blank interval of 200 ms. After this interval the display appeared and the simulated movement of both the observer and walker/object began immediately. After this movement period, the walker/object disappeared from the scene while the ground plane remained visible. A vertical probe line on the horizon of the ground plane appeared at the center of the screen. Observers were asked to use a mouse to move the probe along the horizon to indicate their perceived heading. Observers clicked a mouse button to signal a response which also triggered the start of the next trial.

The four display conditions were run in four separate blocks, with each block containing nine trial duration conditions (100, 150, 200, 250, 300, 350, 400, 450, and 500 ms) presented in a random order. Each duration condition was presented 12 times in each block, resulting in 108 trials per block and 540 trials in total. For the three experimental display conditions, the walker/object moved leftward for half of the trials in every duration condition and rightward for the other half of the trials.

Before the beginning of the experiment, observers were informed that the moving object could appear as either human or nonhuman. The testing order of the four blocks was counterbalanced between observers. Observers were instructed to move as little as possible during the experiment and indicate their perceived heading at the end of each trial regardless of the presence of a walker or an object. Observers received 15 practice trials before beginning the experiment. The normal walker condition was used for the practice trials. The trial duration and walker motion direction were chosen randomly from the nine trial durations and two walking directions for each practice trial. All testing took place in a quiet, darkened room. Observers were seated 1 m from the display at an eye height of 1.4 m. Overall the experiment took approximately 45 min to complete.

Results and discussion

Data for individual observers was initially screened for outliers and other relevant statistical violations. One observer produced average heading errors larger than 2.5 standard deviation from the mean and was thus deemed unable to do the task and excluded from the analysis.

Signed heading errors were used to quantify the bias in heading judgments. Negative errors represented errors to the left of the actual heading, whereas positive errors represented estimates to the right of the actual heading. Thus, for a walker/object moving leftward, negative errors would reflect a bias in the direction of walker/object motion, whereas positive errors would reflect a bias in the opposite direction of walker/object motion. The opposite would be true for rightward-moving walkers/objects. Signed heading errors for each object condition and trial duration are shown in Figure 2.

A 3 (display type) × 9 (duration) × 2 (moving direction) repeated-measures analysis of variance (ANOVA) was conducted on the signed heading errors. The data for the interaction between walker type and trial duration and the interaction between walker type, trial duration, and motion direction violated the assumption of sphericity for ANOVA. Greenhouse-Geisser corrections were applied to account for this violation. A significant main effect of object motion direction was found, $F(1, 17) = 11.71$, $p = 0.003$, $\eta_p^2 = 0.41$. As can be seen in Figure 2, rightward-moving walkers/objects caused heading estimates to be shifted to the right of the actual heading direction (positive errors), whereas leftward-moving walkers/objects caused heading errors to be shifted to the left of the actual heading (negative errors). This occurred for all three experimental display conditions and indicates that heading was biased in the direction of object motion. Main effects of display type, $F(2, 34) = 0.74$, $p = 0.49$, and duration, $F(8, 136) = 0.71$, $p = 0.69$, were nonsignificant. Two way interactions between display type and moving direction, $F(2, 34) = 0.07$, $p = 0.93$; display type and duration, $F(4.84, 82.27) = 0.82$, $p =$

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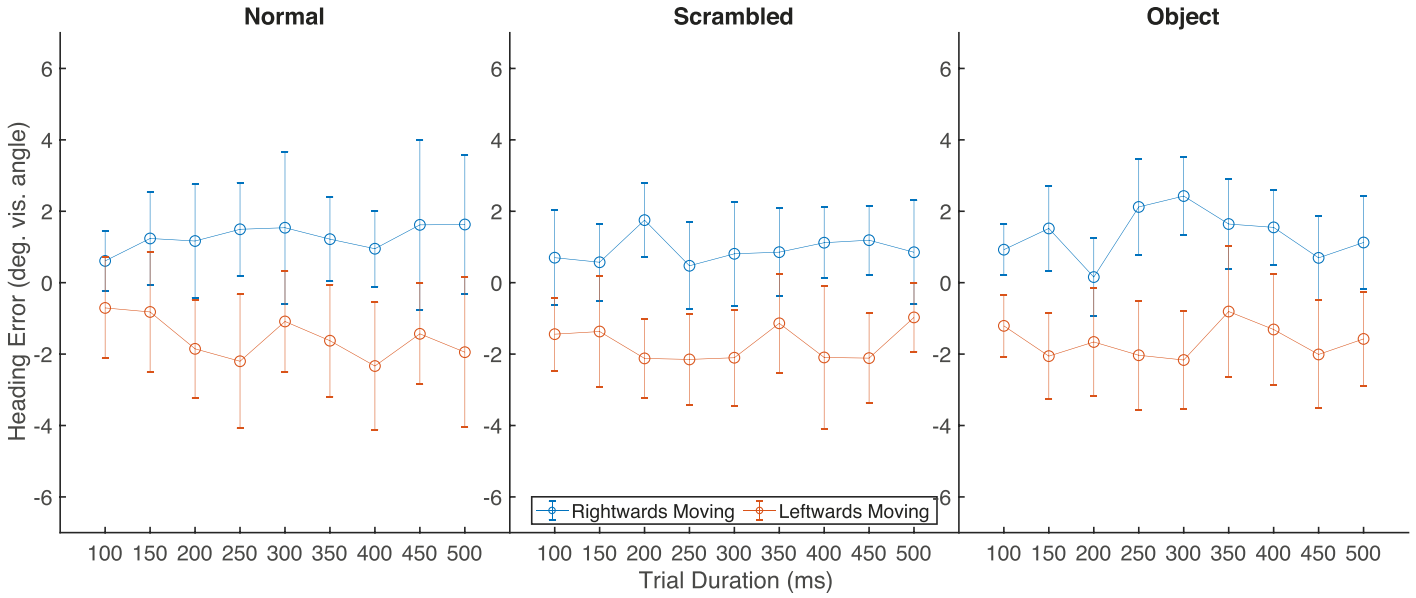

Figure 2. Signed heading errors in the normal walker, scrambled walker, and the laterally moving object conditions. Positive heading errors indicate the perceived heading to the right of the actual heading direction, while negative heading errors indicate the perceived heading to the left of the actual heading direction. Trial duration is shown on the *x*-axis. Vertical bars represent 95% confidence intervals.

0.67; as well as duration and moving direction, $F(8, 136) = 1.75$, $p = 0$ .09, failed to meet statistical significance, so did the three way interaction, $F(5.49, 93.31) = 1.04$, $p = 0.45$. These results suggest that the heading errors were not affected by object type or trial duration.

In addition to the above analysis, we conducted a Bayesian analysis equivalent to a repeated-measures ANOVA to test the hypothesis that PLW walker motion biases heading estimation. Due to the fact that Bayesian models are less dependent on sample size than frequentist models such as ANOVA (S. Y. Lee & Song, 2004), this analysis provides a more quantifiable estimate of the likelihood of the hypothesis that PLWs bias heading estimation over the hypothesis that walkers do not affect heading more than an object with no internal motion. The Bayesian analysis had the same structure as the frequentist ANOVA described in the previous paragraph (3 display types × 9 durations × 2 moving directions) and was run in JASP (JASP Team, 2019) using the default Cauchy prior, with an *r* scale width of 0.5. This analysis serves to yield a Bayes factor, which is the ratio between the evidence for the null and alternative model. A Bayes factor of 1 would indicate a lack of evidence for either the null or alternative hypothesis. Factors greater than 1 indicate evidence in favor of the alternative hypothesis, while factors less than 1 indicate evidence in favor of the null. The further a Bayes factor is away from 1, the stronger the evidence for either the null or alternative hypothesis (Jeffreys, 1961; M. D. Lee & Wagenmakers, 2014). It should be noted that to improve the interpretability of the results in this manuscript we have used logarithms of the Bayes factor. For a more complete discussion of Bayesian analysis and how it applies to a context that is directly comparable to the methods used here, we point the reader to Quintana and Williams (2018), as well as Wagenmakers et al. (2018).

A moving-direction-only model produced the largest Bayes factor ($P(M|data) = 0.99$, $\text{Log}(BF_{10}) = 85.92$) over the null model, indicating a very strong evidence that the motion direction of an object (or walker) influences heading estimation. This is in line with the results produced by the frequentist ANOVA. This model was preferred over a model that included motion direction and display type by a Bayes factor of $\text{Log}(BF_{10}) = -4.23$ and also over a model that included motion direction, display type, and an interaction between the two factors by a Bayes factor of $\text{Log}(BF_{10}) = -6.78$. The data thus provide evidence against the hypothesis that PLWs influence heading perception more than object motion in the environment. Because the motion-direction-only model is the simplest model tested here, the Bayesian analysis results are consistent with the results of the classical frequentist ANOVA.

We next compared the bias produced by the walker/object motion to the no-object baseline condition. Because the bias was not statistically different between the three walker/object conditions, we collapsed the leftward and rightward motion direction data across the three conditions and compared leftward and rightward motion directions to the no-object condi-

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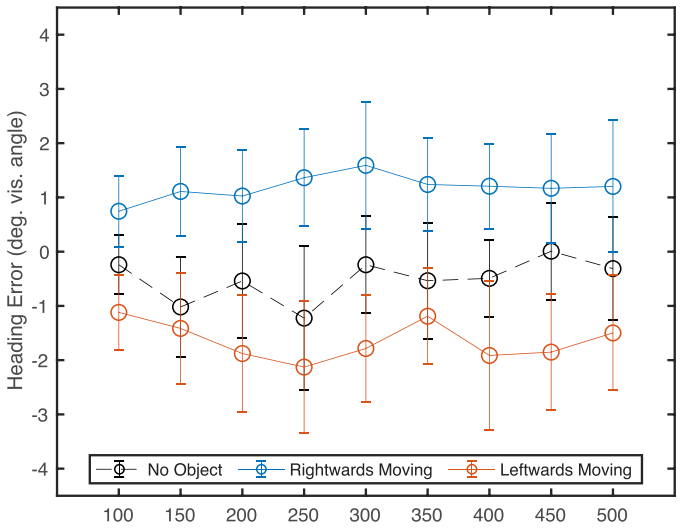

Figure 3. Signed heading errors for rightward and leftward motion compared to the no-object condition. Vertical bars represent 95% confidence intervals.

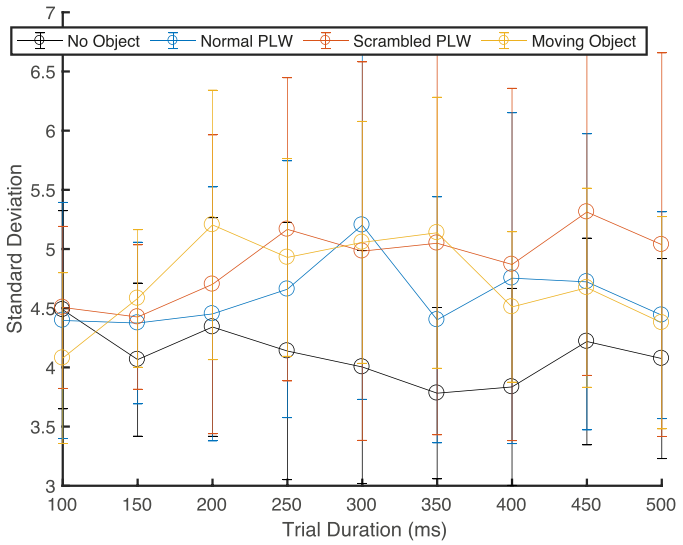

Figure 4. Standard deviations of the signed heading errors against trial duration for each display type. Vertical bars represent 95% confidence intervals.

tion (Figure 3). A 3 (direction: leftward, no object, rightward) × 9 (duration) repeated-measures ANOVA revealed a significant main effect of direction, $F(1,17) = 11.7$, $p = 0.003$, $\eta_p^2 = 0.39$, and no effect of duration nor an interaction. Post hoc t tests with Benjamini-Hochberg adjustment showed significant differences between all three directions (rightward vs. no object: $p < 0.01$, leftward vs. no object: $p = 0.03$, rightward vs. leftward: $p < 0.01$). We also repeated this analysis using Bayesian statistics. A model comprising of direction only produced the largest Bayes factor over the null model (P(M|data) = 0.91, Log(BF_{10}) = 52.9). This is congruent with the results of the frequentist analysis.

Standard deviations of the signed heading errors were used to quantify the precision in heading judgments with the four display types. Standard deviations for the leftward- and rightward-moving objects/walker object conditions were averaged for each observer. The heading precision data for all four display conditions can be seen in Figure 4. A 4 (display type) × 9 (duration) repeated-measures ANOVA was also conducted on the heading precision data. There was a significant main effect of display type, $F(1, 18) = 5.92$, $p = 0.026$, $\eta_p^2 = 0.21$. Smaller standard deviations in the control condition indicate that the precision of heading judgments in the control condition of pure background flow was better than that in the other three display conditions (Bonferroni adjusted post hoc t tests, all p's < 0.001). The other conditions were not different from each other (all p's > 0.05). There was no main effect of trial duration, $F(1, 18) = 1.42$, $p = 0.25$, and no significant interaction between trial duration and display type, $F(1, 18) = 0.13$, $p = 0.72$.

Experiment 2: Heading biases when walkers are away from the FOE

Previous studies found that independently moving objects affected heading judgments only when they obscured or were in close proximity to the FOE of the background optic flow (Layton & Fajen, 2015, 2016a, 2016b; Royden & Hildreth, 1996; Warren & Saunders, 1995). In contrast, Li et al. (2018) showed that independently moving objects can affect heading judgments even when they are not close to the FOE of the background optic flow. In Experiment 2, we sought to test whether normal PLWs and scrambled PLWs could bias heading estimation in a similar way when they are away from the FOE of the background optic flow.

Methods

Observers

Twelve observers were recruited to participate in Experiment 2 (five females, seven males, age: 19–45). All observers had normal or corrected-to-normal binocular vision. One of the observers was an author, while all other observers were naive to the aims of the experiment. All observers gave written informed consent and were rewarded with course credit for their participation.

Materials

The setup used in the current experiment was the same as detailed in the previous experiment.

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Visual display

In the current experiment, the display simulated an observer translating at 1 m/s through a three-dimensional random dot cloud that was generated by randomly distributing points over a frustum that had the size of the display (102.68° V × 90° H) and with a depth of 4 m. The number of points in the flow field was determined by matching the dot density of the flow field to the point density of the walker. Only normal and scrambled PLWs were tested in the current experiment. The laterally moving object condition from Experiment 1 was not tested.

On each trial, the heading direction of the simulated self-motion was randomly selected between 5°–10° to the left or right of the center of the screen. The walker could walk either toward or away from the background FOE. When walkers walked away from the FOE, their starting position was either 5° or 10° from the heading direction, and when walkers walked toward the FOE, their final position was either 5° or 10° from the heading. Leftward-walking walkers would walk toward the FOE if their positions were to the right of the FOE, and away from the FOE if their positions were to the left of the FOE. The opposite was true for rightward-moving walkers. The walker thus did not obscure the FOE at any time during the trial. A blank area in the size of the walker and void of background dots was placed behind the walker, such that none of the background points interspersed the walker at any time during the trial. This was done in order to make the current experiment more comparable to similar experiments, by Li et al. (2018). As in Experiment 1, a control condition with no moving object was also tested. Aside from the lack of a walker, the pure background flow display was the same as the walker plus background display.

Walkers in the current experiment were taken from the motion capture files of seven different actors (three female), who were recorded walking at the speed that felt most comfortable to them (ranging from 0.76–1.2 m/s, mean = 0.96 m/s, $SD = 0.23$ m/s). At their largest size, walkers subtended 10.28° (width) × 18.18° (height). The use of different walkers provided a more naturalistic setting and avoided easy recognition of a standard walker that some subjects in Experiment 1 reported. On each trial, walkers were selected randomly from the set and positioned such that the feet were at a height of 0.9 m below eye level.

Procedure

At the beginning of each trial, a small fixation cross appeared at the center of the screen. After 500 ms, the fixation cross was replaced with the scene and movement began immediately. Movement lasted for 800 ms, after which the walker disappeared and a red probe line appeared in the center of the display. Participants were instructed to move this probe along the horizontal axis to indicate their perceived direction of heading.

Three display conditions were tested: the two walker conditions (normal and scrambled) and the control condition with no moving object. Trials were blocked by display condition, with each block containing 120 trials. For the two walker conditions, each combination of walking direction (left and right) and walker position (5° or 10° on the left or right side of the FOE) was presented 15 times and in a random order in each block. The testing order of blocks was counterbalanced between participants. Prior to beginning the experiment, participants completed 40 practice trials. The normal walker condition was used during practice and the walking direction and the starting position were randomly chosen in each practice trial. In total, the experiment contained 360 trials and took approximately 30 min to complete. All testing took place in a quiet darkened room.

Results and discussion

Data for all observers were checked for outlier performance and relevant statistical violations. No observer was excluded from the analyses. As in Experiment 1, the signed heading errors were used to measure the accuracy of heading judgments. Negative errors represented the perceived heading to the left of the actual heading, whereas positive errors represented the perceived heading to the right of the actual heading. Therefore, for walkers moving leftward, negative errors would indicate a bias in heading judgments in the direction of walking while positive errors would indicate a bias in the opposite direction of walking. The opposite is true for rightward-moving walkers. Signed heading errors for the two walker display conditions are shown in Figure 4.

A 2 (walker type) × 4 (walker position) × 2 (walker motion direction) repeated-measures ANOVA was conducted to assess the signed heading errors produced by normal and scrambled walkers. There was no significant main effect of walker type, $F(1, 11) = 2.21$, $p = 0.17$. However, there were significant main effects of both walker position, $F(3, 33) = 4.38$, $p = 0.01$, $\eta_p^2 = 0.29$, and walker motion direction, $F(1, 11) = 6.00$, $p = 0.03$, $\eta_p^2 = 0.35$. Figure 5 shows that the main effect of walker motion direction reflects a bias in heading judgments in the direction of walker motion. Bonferroni-adjusted post hoc t tests for the main effect of walker position failed to reveal any significant differences between the four walker positions. There was no significant two-way interactions between walker type

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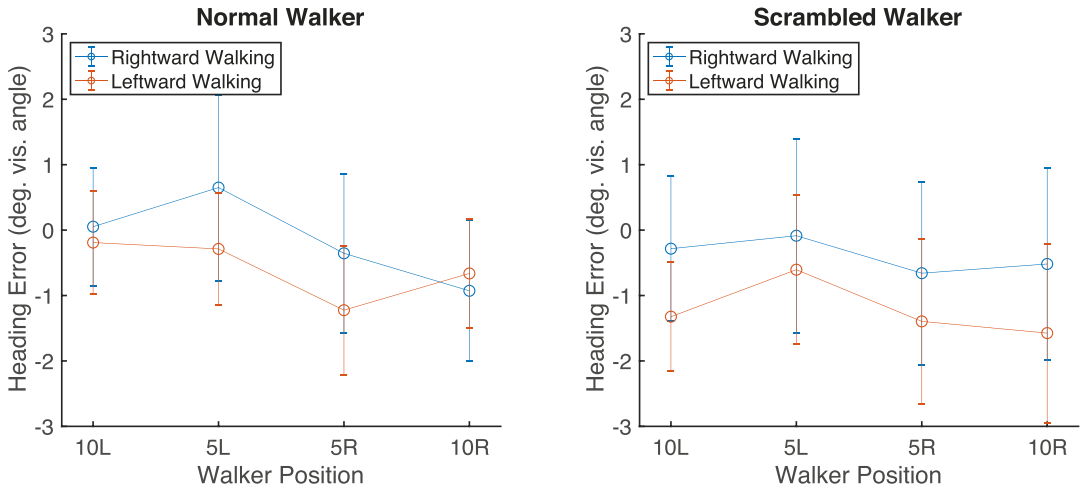

Figure 5. Signed heading errors produced by normal and scrambled PLWs that moved leftward (red lines) or rightward (blue lines). The walker's position, which defines the minimum distance between the walker and the FOE, is shown on the *x*-axis. Leftward-walking walkers would walk toward the FOE if the walker position was on the right (R) and away from the FOE if the walker position was on the left (L). The opposite was true for rightward-walking walkers. Positive heading errors on the *y*-axis indicate the perceived heading to the right of the actual heading, while negative heading errors indicate the perceived heading to the left of the actual heading. Vertical bars represent 95% confidence intervals.

and walking motion direction, $F(1, 11) = 1.67$, $p = 0.22$, walker type and walker position, $F(3, 33) = 0.81$, $p = 0.50$, or walking direction and walker starting position, $F(3, 33) = 0.41$, $p = 0.75$. There was a significant three-way interaction, $F(3, 33) = 3.69$, $p = 0.02$, $\eta_p^2 = 0.25$. In Figure 5, normal walkers appeared to produce less heading bias at the two extreme walker positions than scrambled walkers. Bonferroni-adjusted post hoc tests gave a significant difference between leftward- and rightward-moving walkers at the 10° right position for scrambled walkers ($p = 0.02$) but not for normal walkers.

A Bayesian analysis equivalent to the repeated-measures ANOVA revealed that a model with the main effects of display type, motion direction, and object position but no interactions produced the largest Bayes factor compared to a null model ($\text{Log}(\text{BF}_{10}) = 6.12$), indicating that there is moderate evidence that all three factors influence heading estimation. This differs somewhat from the frequentist ANOVA analysis results, which found no significant main effect of walker type but showed a significant three-way interaction. Since, the Bayes analysis did not support any interaction we consider the finding of the three-way interaction in the frequentist ANOVA as unstable. The main effect of walker type found in the Bayes ANOVA corresponds to a slightly more leftward bias for scrambled compared to normal walkers. This, however, is unrelated to our main question whether bias is smaller for normal than for scrambled walkers, which would imply an interaction between walking direction and display type.

As in Experiment 1, we examined whether walker types affected the precision of heading judgments by computing the standard deviation of the signed heading errors. Figure 6 plots the standard deviation data for the normal walker, the scrambled walker, and the no-moving–object display conditions. Standard deviations for the leftward- and rightward-moving objects/walker object conditions were averaged for each observer.

A one-way repeated-measures ANOVA was conducted to compare precision in heading judgments in the three display conditions. The precision of heading judgments did not differ between the three display conditions, $F(1, 11) = 2.09$, $p = 0.18$.

General discussion

Previous studies have shown that when an independently moving object is present in a scene, heading estimation is biased by the object's lateral motion (Layton & Fajen, 2015, 2016b; Li et al., 2018; Royden & Hildreth, 1996; Warren & Saunders, 1995).

The aim of the current study was to examine whether biological motion biases heading estimation from optic flow when a PLW moves through a scene. Walkers are visually complex, as they are comprised of multiple articulated parts that signal information about an actor's movement in the scene. Theoretically, this biological motion information could be used to provide cues about human figures in the environment and can thus help segment moving human figures from optic flow. Indeed, previous research has revealed that

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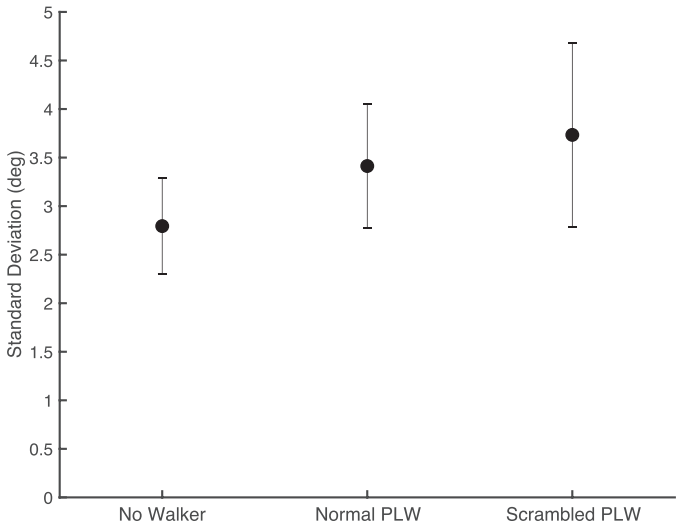

Figure 6. Standard deviation of the signed heading errors for the normal walker, the scrambled walker, and the no-moving-object display conditions. Vertical bars represent 95% confidence intervals.

biological motion is highly salient during self-motion and can be integrated to form behavioral plans or detect pedestrians (Fotios, Uttley, & Yang, 2015; Jovancevic-Misic & Hayhoe, 2009). However, despite the marked differences between PLWs and laterally moving objects composed of random dots, we did not observe any difference in the heading bias produced by normal walkers, scrambled walkers, and simple moving objects. This suggests that biological motion is not used to segment moving human figures from optic flow prior to heading perception during self-motion. The object motion component is computed similarly for walkers and objects with no limb motion, and biological motion is inconsequential at least for heading perception. These results are in line with the findings of Li et al. (2018) in that the visual system can identify independent moving objects in the scene but pools motion from the entire flow field for the analysis of self-motion heading estimation (Li et al., 2018). Biases in different directions relative to object motion direction (Li et al., 2018; Royden & Hildreth, 1996; Warren & Saunders, 1995) can be explained by a full analysis of translational and rotational self-motion components in the pooled flow field and a lack of object segmentation.

This conclusion is corroborated by the results of our other study (Riddell & Lappe, 2017) that also measured self-motion perception using stimuli that combined biological motion with optic flow. Specifically, the stimuli showed a single 12-point walker that approached the observer. No ground plane was visible. In some trials, the observer was stationary so that the motion of the dots presented only the motion of the walker towards the observer. Other trials added a simulated forward motion of the observer. In those trials, the motion of each point in the 12-point walker was a combination of walker motion and observer motion. Participants were well able to discriminate these two trial types and, hence, identify the presence of simulated self-motion in addition to walker motion. However, when they were asked to estimate their heading in trials, which contained combined self-motion and walker motion, systematic heading errors occurred. These errors indicate that heading estimates were computed by pooling all motion vectors in the visual field without taking walker motion into account.

Previously Cutting et al. (1995) found no bias in heading estimation with scenes containing walkers, even when walkers intersected the FOE. Given the results of the current study showing that walkers do bias heading estimation, we suspect that the results obtained by Cutting et al. (1995) are unlikely due to biological motion processing. Instead, we propose that the lack of bias may be due to the fact that they used an optic flow field that contained highly regular environmental structure and stable reference objects, which could have facilitated the perception of heading (e.g., Cutting et al., 1995; Cutting & Wang, 2000; Li & Warren, 2000).

The bias in heading judgments observed in both previous studies and the current study is small (within the range of a few degrees). As such, it may simply be the case that it is more efficient for the visual system to treat walkers in the same way as nonarticulated objects rather than spend resources integrating biological motion information for minimal gain.

Although biological motion does not appear to enable accurate heading detection in the presence of an independently moving object, it may play a role in more directly relevant tasks like object detection, avoidance, or interception. In fact, Riddell and Lappe (2017) found that observers use biological motion information to identify the separate walker motion and self-motion components in a scene. Rushton, Chen, and Li (2018) also found that the ability to identify object motion is not limited by, or yoked to, the ability to perceive heading during self-motion. These findings support the proposal that the identification of object motion and the perception of heading during self-motion involves separate visual pathways (Rushton, Niehorster, Warren, & Li, 2018). Similarly, the identification of biological motion has also been shown to be distinct from the perception of optic flow (Beintema & Lappe, 2002) and involving separate visual pathways (Grossman et al., 2000; Michels, Lappe, & Vaina, 2005) and mechanisms (Lange & Lappe, 2006; Mayer et al., 2019; Theusner et al., 2014).

A common finding of the present study and related recent works (Li et al., 2018; Riddell & Lappe, 2017, 2018) is that the computation of heading from optic flow is insensitive to object motion in the environment

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and uses all visual motion as if it were resulting from a stationary world. Perhaps this is a cost to pay to keep the computation of heading fast and simple. Segmentation of moving objects and identification of biological motion are complex computational problems that take time. If heading computation needs to be fast to control action, the benefits of being fast and accepting a small bias may outweigh the cost of improving the heading estimate by segmenting moving objects or people.

Keywords: optic flow, heading, biological motion

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