Attractive serial dependence in heading perception from optic flow occurs at the perceptual and postperceptual stages

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Previous work has revealed that the heading perception from optic flow can be either attracted to the straight-ahead direction showing a center bias or repelled away from the previously seen heading (i.e., repulsive serial dependence) after ruling out the center bias accounting for perceptual errors. Recent studies have debated whether the serial dependence occurs at the perceptual or postperceptual stages (e.g., working memory). Our current study reexamined the serial dependence in heading perception and investigated whether the serial dependence occurred at perceptual or postperceptual stages. Additionally, an ideal observer model was developed to explore whether observers optimally combined the straight-ahead direction and previous and current headings to perceive headings. Our results showed that after ruling out the center bias, the perceived heading was biased toward the previous heading, suggesting an attractive serial dependence in heading perception. This attractive serial dependence occurred at both perceptual and postperceptual stages. Importantly, the perceived heading was well predicted by an ideal observer model, suggesting that observers could optimally combine their perceptual observations (current heading) with their prior information about the straight-ahead direction and previous headings to estimate their heading.
size of center bias increased with the decrease of the reliability of optic flow, consistent with a Bayesian inference account or an ideal observer model in which the straight-ahead direction worked as a prior (also see Xing & Saunders, 2016). Additionally, the current trial’s perceived heading was biased toward the previously seen heading, showing an attractive serial dependence (Sun et al., 2020). Previous work proposed that the attractive serial dependence could help observers keep the world continuity by reducing the ability to discriminate fine differences (Fischer & Whitney, 2014). However, after removing the heading error caused by the center bias from the perceived heading error, the residual perceived headings were biased away from the previously seen headings, showing a repulsive serial dependence. Sun and his collaborators proposed that the repulsive serial dependence could help the visual system detect small stimuli changes, improving perception sensitivity (Gepshtein, Lesmes, & Albright, 2013). Their results also showed that the size of repulsive serial dependence increased with the decrease of the reliability of optic flow, following the prediction of an ideal observer model in Cicchini, Mikellidou, and Burr (2018).

Crowell and Banks (1993, 1996) found that the threshold of heading discrimination increased with the heading eccentricity, suggesting that the reliability of optic flow decreased with the increase of heading eccentricity. According to the Bayesian inference theory (Bernardo & Smith, 1994; Jaynes, 1986; MacKay, 2003) and the ideal observer theory (see Geisler, 2011, for review), the visual system would rely more on prior (e.g., straight-ahead direction) as the reliability of optic flow decreased. Thus, the size of center bias increased with the heading eccentricity. However, Sun et al. (2020) fitted the perceived heading as a linear function of the actual heading, assuming that the size of the center bias was constant with the heading eccentricity. The linear model overestimated the size of the center bias for the central headings while underestimating the size of center bias for the peripheral headings (see Figures 2b in Sun et al., 2020). After ruling out the center bias predicted by a linear function, the residual heading errors could be from the estimation loss of center bias instead of serial dependence. Therefore, the finding of the repulsive serial dependence revealed by Sun et al. (2020) should be further examined.

Apart from examining the serial dependence in various feature perception tasks—for example, orientation (Ceylan, Herzog, & Pascucci, 2021; Cicchini, Mikellidou, & Burr, 2017, 2018; Fischer & Whitney, 2014; Fritsche, Mostert, & de Lange, 2017; Pascucci et al., 2019; Samaha, Switzky, & Postle, 2019), spatial position (Bliss, Sun, & D’Esposito, 2017), expression, identity and attractiveness of faces (Kim, 2021; Liberman, Fischer, & Whitney, 2014; Taubert, Van der Berg, & Alais, 2016; Xia, Leib, & Whitney, 2016), and numerosity (Fornaciai & Park, 2018)—recent serial dependence studies also debated on the occurrence mechanisms of serial dependence. That is, does the serial dependence occur at the perceptual or postperceptual stages? Several studies found that serial dependence occurred at the perceptual stage (Cicchini et al., 2017; Fischer & Whitney, 2014; Manassi, Liberman, Kosovicheva, Zhang, & Whitney, 2018), but other studies showed the involvement of postperceptual stages (i.e., working memory, decision-making) (Bae & Luck, 2020; Bliss, Sun, D’Esposito, 2017; Ceylan, Herzog, & Pascucci, 2021; Fritsche, Mostert, & de Lange, 2017; Pascucci et al., 2019). In contrast, none of the above studies investigated the occurrence mechanisms of the serial dependence in heading perception from optic flow.

In the current study, we first conducted two experiments to examine whether the serial dependence in heading perception from optic flow was repulsive or attractive. Additionally, we explored whether the serial dependence occurred at the perceptual or postperceptual stages. In Experiment 3, we varied the dot density of optic flow to manipulate the optic flow reliability and developed an ideal observer model to directly examine whether the visual system optimally combined the observations (current heading) with their prior information about the straight-ahead direction and previous heading to perceive heading.

### Experiment 1: Attractive serial dependence in heading perception from optic flow

The current experiment tested the hypothesis that there was serial dependence in the heading perception from optic flow. If there was a serial dependence, then we would naturally ask whether the serial dependence was attractive or repulsive. We also investigated whether the serial dependence occurred at perceptual or postperceptual stages (e.g., working memory).

In this experiment, participants finished three blocks of trials. Each block corresponded to one experimental condition: baseline, perceptual, and postperceptual conditions. On each trial of the baseline condition, one heading stimulus was presented after a blank display, and participants were asked to judge the heading direction of the heading stimulus. On each trial of the perceptual and postperceptual conditions, two heading stimuli were sequentially presented, and participants were asked to judge the heading direction of the second stimulus, whereas in the postperceptual condition, participants were also asked to judge the heading direction of the first stimulus after the response.
to the second stimulus—a classical working memory dual-task paradigm. Therefore, only one heading stimulus was presented on one trial of the baseline condition, whereas two heading stimuli were presented on one trial of the perceptual and postperceptual conditions. We proposed that the heading error was mainly caused by the attractive effect of straight-ahead direction (i.e., center bias) and the effect of headings in previous trials (i.e., between-trial serial dependence) in the baseline condition. In contrast, in the perceptual and postperceptual conditions, the heading error of the second stimulus was caused by the center bias, the between-trial serial dependence, and the effect of headings in the current trial (i.e., within-trial serial dependence). Hence, the differences in heading error between the perceptual (postperceptual) and baseline conditions could be attributed to the within-trial serial dependence. Here, we named the differences in heading error as the residual heading error (RHE). We also calculated the distance between the \( n \)th \((n = 1, 2, \text{etc.})\) previous and current heading, named relative heading (RHI). To evaluate the size of the serial dependence, we fitted the residual heading error as a linear function of the relative heading. A positive slope of the linear function represented an attractive serial dependence in heading perception, suggesting that the perceived heading was biased toward the heading direction of the previous stimulus. In contrast, a negative slope represented a repulsive serial dependence, suggesting that the perceived heading was biased away from the heading direction of the previous stimulus. Additionally, a slope significantly different from zero indicated the existence of the serial dependence in the perceptual stage. Next, to explore whether the serial dependence occurred at the postperceptual stages, we compared the slopes of the fitted lines in the perceptual condition with the postperceptual conditions. If the slopes were significantly different between the two conditions, then the serial dependence occurred at the postperceptual stage.

With the current experimental design, the hypothesis that center bias was constant or varied along with the heading eccentricity did not affect the serial dependence, different from Sun et al. (2020), which assumed a constant size of the center bias across different heading eccentricities.

**Methods**

**Participants**

Eighteen participants (6 males and 12 females; age: 19–28 years) were enrolled from Zhejiang Normal University. They were with corrected or correct-to-normal vision and naive to the purpose of the experiment. The experiment was approved by the Scientific and Ethical Review Committee in the Department of Psychology of Zhejiang Normal University.

**Stimuli and apparatus**

The display (80° H x 80° V; luminance: 0.24 cd/cm²) simulated observers translating at 1 m/s in a three-dimensional dot-cloud space (depth range: 0.20–5 m) consisting of 90 dots (diameter: 0.28°; luminance: 22.5 cd/cm²) (Figure 1a). The simulated self-motion direction (i.e., heading direction) was selected from ±30°, ±25°, ±20°, ±15°, ±10°, ±5°, or 0°. Positive and negative values corresponded to the headings to the right or left of the display center (i.e., 0°).

The displays were programmed in MATLAB using the Psychophysics Toolbox 3 and presented on a 27-in. Dell monitor (resolution: 2,560 H x 1,440 V pixels; refresh rate: 60 Hz) with an NVIDIA GeForce GTX 1660Ti graphics card.

**Procedure**

All participants sat in a light-excluded room and viewed the display monocularly with their heads stabilized with a chinrest. The viewing distance was 20 cm. Participants were asked to fixate on the display center throughout the experiment and keep their straight-ahead direction aligned with the display center.

Each participant was asked to conduct three blocks of trials. Each block corresponded to one condition (e.g., baseline, perceptual, or postperceptual conditions). Figure 1c illustrates the trial procedures of the three conditions. Specifically, each trial of the baseline condition started with a blank display, lasting for 700 ms, followed by a 500-ms heading stimulus. The heading direction of the stimulus was randomly selected from ±20° or ±10°. After the heading stimulus, a display was presented with a horizontal line in the midsection of the display. Participants were asked to move a mouse-controlled probe to indicate their perceived heading along the horizontal line. When the participants clicked the mouse button, a blank display was presented for 1,200 ms. The trial procedure of the perceptual condition was similar to that of the baseline condition, except that two 500-ms heading stimuli were sequentially presented, separated by a 200-ms blank display. The heading of the second stimulus was randomly selected from ±20° or ±10°; the heading of the first stimulus was left or right of the heading of the second stimulus by 5° or 10°. Participants were asked to judge the heading of the second stimulus, followed by a 1,200-ms blank display. The trial procedure of the postperceptual condition was similar to that of the perceptual condition, except a 200-ms blank display was presented after the response to the second stimulus, and then participants were asked to judge the heading of the first stimulus.
Figure 1. (a, b) Schematic illustration of visual stimuli used in the current study. The displays simulated observers translating in a three-dimensional dot cloud space consisting of 90 dots (Experiments 1 and 2) and 45 or 135 dots (Experiment 3). The figure shows the case where the observers’ self-motion direction (i.e., heading) is right to the display center (0°) by 20°. The white dots show the dots’ positions in first frame of the display. The white lines, invisible in the experiments, represent the dots’ motion trajectories in the following frames. (c) Trial procedure illustrations of three conditions in Experiment 1. Each trial of the baseline condition started with a 700-ms blank display, followed by a 500-ms heading stimulus. Participants were then asked to report their perceived heading by moving a mouse-controlled blue probe. A 1,200-ms blank display was presented after their response. Each trial of the perceptual condition started with a 500-ms heading stimulus, followed by a 200-ms blank display. Then, another 500-ms heading stimulus was presented. The heading direction of the first stimulus was left or right of the heading direction of the second stimulus by 5° or 10°. Participants were asked to report the heading direction of the second stimulus by moving a mouse-controlled blue probe. After their response, a 1,200-ms blank display was presented. The trial procedure of the postperceptual condition was similar to that of the perceptual condition, except that a 200-ms blank display was presented after the response to the second stimulus; participants were then asked to report the heading direction of the first stimulus by moving a mouse-controlled blue probe.

The baseline condition contained four heading directions (±20° and ±10°). Each direction was repeated 60 times, so there were 240 trials. The perceptual and postperceptual conditions contained 4 relative headings (±5° and ±10°) × 4 heading directions (±20° and ±10°), a total of 16 combinations. Each combination was repeated 15 times, so there were 240 trials. All trials were randomly presented in each condition. The conducting sequences of the three conditions (i.e., blocks) were counterbalanced among participants. Before starting the experiment, participants were given 20 practice trials randomly selected from the baseline condition block. The whole experiment lasted for about 30 min.

Data analysis

Center bias: We recorded the perceived headings of all trials. For each condition, we first fitted the perceived heading (PH) as a linear function of the actual heading (AH) for each participant (the AH was the second heading stimulus in each trial of the perceptual and postperceptual conditions), given as

\[ PH = s_{CB} \times AH + error, \]

in which \( s_{CB} \) represented the slope caused by center bias. Specifically, if \( s_{CB} \) was smaller than 1, then the perceived heading was smaller than the actual heading, indicating a center bias was in the heading perception from optic flow.

To examine whether participants followed the instruction to memorize the heading direction of the first stimulus in the postperceptual condition, we fitted a linear function (Equation 1) between the perceived and actual headings of the first stimulus. If the slope was significantly greater than 0, then perceived headings increased with actual headings, indicating that participants followed the instruction to memorize the heading of the first stimulus.

Serial dependence before ruling out center bias: Like Sun et al. (2020), we first analyzed the serial dependence before ruling out center bias in heading perception. We calculated the heading error (HE) and the relative heading (RH), given as

\[ HE = s_{SD} \times RH + error, \]

where the heading error (HE) was the difference between the perceived and actual headings of current heading stimuli. The relative heading (RH) was the relative distance between the actual heading in the nth (n = 1, 2, etc.) previous and current stimuli. A negative \( s_{SD} \) suggested a repulsive serial dependence was in heading perception. In contrast, a positive \( s_{SD} \) suggested an attractive serial dependence was in heading perception.
Serial dependence after ruling out center bias: Next, we examined the serial dependence after ruling out center bias by calculating the residual heading error \((RHE)\). The residual heading error included the differences in the perceived heading between the perceptual (postperceptual) and baseline conditions. We fitted the residual heading error as a linear function of the relative heading \((RH)\), given as

\[
RHE = s_{SD} \times RH + error. \quad (3)
\]

A positive \(s_{SD}\) suggested an attractive serial dependence in heading perception. In contrast, a negative \(s_{SD}\) suggested a repulsive serial dependence. The absolute value of \(s_{SD}\) reflected the size of the serial dependence. The larger the absolute value of \(s_{SD}\), the larger the serial dependence. Additionally, if the \(s_{SD}\) of the perceptual condition was significantly different from 0, then the serial dependence occurred at the perceptual stage. If the \(s_{SD}\) in the postperceptual condition was significantly different from that in the perceptual condition, then the serial dependence occurred at the postperceptual stage.

Note that there were two headings sequentially presented in each trial of the perception and postperceptual conditions, but only one heading was in the baseline condition after a blank display. Therefore, the heading stimulus in the \(n\)th trial of the baseline condition corresponded to the second heading stimulus in the \(n\)th trial of the perceptual and postperceptual conditions. The heading in the \(n\)−1th trial of the baseline condition (i.e., first previous heading) corresponded to the second heading in the \(n\)−trial of the perceptual and postperceptual conditions (i.e., second previous heading). Since the previous headings were in different trials from the current heading, these previous headings were named between-trial preheadings. Additionally, in the perceptual and postperceptual conditions, the first previous heading stimulus and the current heading stimulus were in the same trial. These previous headings were named within-trial preheadings.

Moreover, in the above analysis, the \(RH\) was the difference in the actual heading between the previous \(n\)th \((n = 1, 2, \text{etc.})\) trial and the current trial. In this analysis, for the trials where participants also responded to the \(n\)th previous heading stimulus, we replaced the \(RH\) with the \(PRH\) that was the difference between the perceived heading of the previous \(n\)th \((n = 1, 2, \text{etc.})\) heading stimulus and the actual heading of the current heading stimulus, given as

\[
RHE = s_{SD} \times PRH + error \quad (4)
\]

\(RHE\) was the mean of residual heading errors in each bin with a width of 5° within the range of \([-57.5°, 57.5°]\). This analysis also examined whether the serial dependence occurred at the postperceptual stages. However, what differed from relative heading in Equation 3 was that the perceived relative heading in Equation 4 might include working memory and decision-making. That is, Equation 4 revealed more complex postperceptual stages than Equation 3. If the value of \(s_{SD}\) was significantly different from the value of \(s_{SD}\) in the perceptual condition and significantly different from 0, then the serial dependence occurred at the postperceptual stage.

Results

Figure 2 plots the mean perceived heading averaged across participants against the actual heading in different conditions. In the baseline condition, perceived headings were attracted to the straight-ahead direction, showing a center bias (Figure 2a), which was also observed for the estimation of second heading stimuli in the perceptual and postperceptual conditions (Figures 2b, 2c). To evaluate the center bias effect, we fitted the perceived heading as a linear function of the actual heading (Equation 1). The linear regression analysis showed that the fitted lines accounted for over 99.7% variance in the perceived headings. A one-sample \(t\) test revealed that the slope \((s_{CB})\) of the fitted line was significantly below 1 \((t(17) = -3.47, p < 0.0029, \text{Cohen’s } d < 1.15)\), indicating significant center bias effects.

Figure 2d plots the perceived heading of the first stimulus in the postperceptual condition. It shows that the perceived heading increases with the actual heading. The linear regression analysis showed that the fitted line accounted for 98.4% variance in the perceived headings. A one-sample \(t\) test revealed that the slope \((s_{CB})\) of the fitted line was significantly larger than 0 \((t(17) = -17.39, p < 0.001, \text{Cohen’s } d = 5.80)\), suggesting that participants followed the instruction to memorize the heading of the first stimulus in the postperceptual condition.

Figure 3 plots the results of serial dependence before ruling out center bias. The x-axis (y-axis) is the relative heading (heading error). Figure 3a shows the serial dependence of the first and second previous headings in the baseline condition; Figures 3b and 3c show the serial dependence of the first, second, and third previous headings in the perceptual and postperceptual conditions. They clearly show that in all conditions, when the previous heading is left to the current heading (i.e., the relative heading was negative), the perceived heading is left to the actual heading (i.e., the heading error was negative) and vice versa. This suggests that the perceived heading is biased toward the previous heading, indicating an attractive serial dependence in heading perception. To evaluate the serial dependence, we fitted the heading error as a linear function of the relative heading (Equation 2). The linear regression
analysis showed that the fitted lines accounted for over 95.6% variance in the heading error. One-sample $t$ test revealed that the slope ($s_{SD}$) of the fitted line was significantly larger than 0 ($t(17) > 3.89, p_s < 0.001$, Cohen’s $d_s > 1.30$), indicating a significant attractive serial dependence in heading perception.

Paired samples $t$ test showed that the slopes ($s_{SD}$) were not significantly different between the first and second previous headings in the baseline condition ($t(17) = -0.56, p = 0.58$, Cohen’s $d_s > 1.30$), suggesting a robust serial dependence in the baseline condition.

One-way repeated-measures analysis of variance (ANOVA) (3 previous headings) analysis showed that the main effects of previous headings were significant in the perceptual (Greenhous–Geisser corrected: $F(1.00, 17.08) = 7.85, p = 0.012, \eta^2 = 0.32$) and postperceptual (Greenhous–Geisser corrected: $F(1.00, 17.07) = 9.11, p = 0.0077, \eta^2 = 0.35$) conditions. Newman–Keuls post hoc analysis showed that in the two conditions, the $s_{SD}$ of the first previous heading was significantly larger than that of the second and third previous headings ($ps < 0.0036$), while the difference in the $s_{SD}$ was not significant between the second and third previous headings ($p > 0.60$). These results suggested that the size of the serial dependence decreased with the increase of the interval time between the previous and current stimuli in the perceptual and postperceptual conditions.

Figure 4 plots the results of serial dependence after ruling out center bias. In all figures, the y-axis is the residual heading error that was the difference in the perceived heading between the perceptual (or postperceptual) and baseline conditions. In Figures 4a and 4b, the x-axis was the relative heading, meaning the difference in the actual heading between the $n$th ($n = 1, 2, \ldots$) previous and current stimuli. In Figures 4c and 4d, the x-axis was the perceived relative heading ($PRH$), meaning the difference between the perceived heading of the $n$th previous stimuli and the actual heading of current stimuli. It clearly shows attractive serial dependence in the first previous heading. The linear regression analysis showed that the fitted line accounted for over 42.5% variance in the residual headings. One-sample $t$ test showed that the $s_{SD}$ and $s'_{SD}$ were all not significantly different from 0 ($ts(17) < 1.56, ps > 0.14$, Cohen’s $d_s < 0.52$) in the second and third previous headings. These results suggest that the serial dependence occurred within one trial and disappeared across the trials after ruling out the center bias. Additionally, the significant serial dependence in the perceptual condition suggested that the serial dependence occurred at the perceptual stage.

Paired samples $t$ test showed that there was no significant difference in the $s_{SD}$ of the first previous heading between the perceptual and postperceptual
Figure 3. Results of serial dependence before ruling out center bias in Experiment 1. The x-axis was the relative heading that was the difference in the actual heading between the nth (n = 1, 2, etc.) previous and current stimuli. “Left” and “Right” on the x-axis mean that the nth previous heading stimulus’s actual heading was left or right of the current heading stimulus’s actual heading. The y-axis was the heading error that was the difference in the perceived heading and actual heading of the current heading stimulus. “Left” and “Right” on the y-axis mean that the perceived heading of the current heading stimulus was left or right of the actual heading.

Each circle represents the mean heading error averaged across 18 participants; the error bar represents the standard error across 18 participants. The horizontal dashed line represents no serial dependence in the heading perception. The solid line shows the best linear fitting result. The small panel on the top-right corner shows the averaged slope (diamond marker) and the slopes of 18 participants (light color dots). Panels (a) to (c) show the results of the serial dependence in the baseline, perceptual, and postperceptual conditions. *0.01 < p < 0.05; **0.001 < p < 0.01; ***p < 0.001.

condition (t(17) = 0.72, p = 0.48, Cohen’s d = 0.21) and between the s of the perceptual condition and the s’ of the postperceptual condition (t(17) = 1.56, p = 0.14, Cohen’s d = 0.46). These suggested that the serial dependence did not occur at the postperceptual stage. Additionally, the difference between the s and s’ of the postperceptual condition was not significant (t(17) = 0.18, p = 0.86, Cohen’s d = 0.030), suggesting that the previously perceived heading did not cause a stronger serial dependence than the previous actual heading.
Serial dependence after factoring out center bias

**Figure 4.** Results of serial dependence after ruling out center bias in **Experiment 1**. In (a) and (b), the x-axis is the relative heading, meaning the difference in the actual heading between the nth (n = 1, 2, etc.) previous and current headings. In (c) and (d), the x-axis is the perceived relative heading, meaning the difference between the perceived heading of the nth stimulus and the actual heading of the current stimulus. The y-axis was the residual heading error that was the difference in the perceived heading between the perceptual (or postperceptual) and the baseline condition. “Left” and “Right” on the x-axis mean that the nth previous heading
Discussion

The current experiment found that the perceived headings were systematically compressed toward the display center, showing a center bias in heading perception and bias toward the previously seen headings before ruling out the center bias, showing an attractive serial dependence. Additionally, the serial dependence would last for multiple seconds. These results were consistent with Sun et al. (2020).

However, after ruling out the center bias by subtracting the perceived heading of the baseline condition from the perceived heading of the perceptual and postperceptual conditions, there was a robust attractive serial dependence in the first previous heading, rather than a repulsive serial dependence revealed by Sun et al. (2020). Moreover, this attractive serial dependence existed within one trial but disappeared between trials. Sun et al. (2020) found that the repulsive serial dependence existed between trials. We analyze the differences in the general discussion part. Meanwhile, the results showed that the perceived heading of the previous stimuli did not cause a stronger serial dependence than the actual heading of the previous stimuli, which might suggest that the decision-making stage might not be involved in the serial dependence in heading perception.

Importantly, the current results showed that the serial dependence occurred only at the perceptual stage. The postperceptual stage was not involved in the heading perception. This supported that heading perception was perceptual (Xing & Saunders, 2016).

Experiment 2: Serial dependence in heading perception occurs at the perceptual stage

Experiment 1 found an attractive serial dependence in heading perception, which occurred at the perceptual stage rather than at the postperceptual stage. However, the design of Experiment 1 prevented us from ruling out the possibility that the serial dependence might also happen in the postperceptual stages. Specifically, two heading stimuli were sequentially presented, separated by a blank display on each trial of the perceptual condition. Participants were asked to judge the heading direction of the second heading stimulus in each trial. In contrast, we replaced the first heading with a blank display on each trial of the baseline condition. We proposed that the residual heading error—the difference in the perceived heading between the perceptual and baseline conditions—originated from the perceptual stage. However, some participants might pay attention to the heading direction of the first heading stimulus and keep it in their mind, which led to the postperceptual stages being involved in the perceptual condition. As a result, the finding that the serial dependence did not occur at the postperceptual stage needed to be reexamined.

Participants were asked to finish four blocks of trials to address the above question in the current experiment. Each block corresponded to one condition: perceptual baseline, perceptual load, postperceptual baseline, and postperceptual load conditions. On each trial of the perceptual baseline condition, two integers were first presented on the display center. Participants were asked to add the two integers and keep the sum in their minds. After a blank display, one heading stimulus was presented. Participants were then asked to judge the heading direction. After the response, a new integer was presented on the display center, and participants clicked the mouse button to report whether the previous sum was larger than the current integer. The procedure of each trial in the perceptual load condition was the same as the perceptual baseline condition, but the two integers were presented in the center of one heading stimulus. In both conditions, participants paid attention to the integer adding task, leading to the heading perception of the first stimulus being inhibited in the perceptual load condition. Hence, the residual heading error (i.e., the difference in the perceived heading between the two conditions) was more perceptual than in Experiment 1. If there was a serial dependence, then the serial dependence occurred at the perceptual stage. The procedures of the postperceptual baseline and load conditions were the same as the baseline and postperceptual conditions in Experiment 1. Therefore, the residual heading error (i.e., the difference in the perceived heading between the two conditions) was perceptual and postperceptual. If the size of the serial
dependence in the postperceptual condition was larger than that in the perceptual condition, then the serial dependence occurred at the postperceptual stages.

Methods

Participants

Twenty participants (6 males and 14 females; age: 18–24 years) were enrolled from Zhejiang Normal University. They were with corrected or correct-to-normal vision and naive to the purpose of the experiment. The experiment was approved by the Scientific and Ethical Review Committee in the Department of Psychology of Zhejiang Normal University. They were with corrected or correct-to-normal vision and naive to the purpose of the experiment. The experiment was approved by the Scientific and Ethical Review Committee in the Department of Psychology of Zhejiang Normal University.

Stimuli and apparatus

The stimuli and apparatus were similar to Experiment 1, except the headings were selected from ±30°, ±20°, ±10°, or 0°. Positive and negative values corresponded to the headings to the right or left of the display center (i.e., 0°). In the perceptual baseline and load conditions, each trial started with two integers (RGB: [0 0 50]; visual angle: 1.71° V × 2.29° H) vertically arranged on the display center with a 0.57° gap and randomly selected from the range of [0, 10]. The trial ended with a new integer presented on the display center and selected from the range of [5, 20].

Procedure

The participants’ preparation work was the same as in Experiment 1. Each participant was asked to conduct four blocks of trials. Each block corresponded to one condition: perceptual baseline, perceptual load, postperceptual baseline, or postperceptual load conditions. The trial procedures of the latter two conditions were the same as the baseline and postperceptual conditions in Experiment 1.

On each trial of the perceptual baseline condition, two integers vertically arranged on the display center were first presented for 500 ms. Participants were asked to add the integers and keep the sum in their minds. Then a 200-ms blank display was presented, followed by a 500-ms heading stimulus. The heading direction was randomly selected from ±20°, ±10°, and 0°. After the heading stimulus, a display with a horizontal line that appeared in the midsection of the display was presented. Participants were asked to move a mouse-controlled probe to indicate their perceived heading along the horizontal line. After the response, a new integer was presented on the display center, and participants were asked to click the mouse button to judge whether the previous sum was larger or smaller than the current integer. After the click, the next trial started.

The procedure of each trial in the perceptual load condition was similar to that in the perceptual baseline condition, except the trial started with two integers that were presented in the center of a heading stimulus. The heading direction of the stimulus was left or right of the heading direction of the second stimulus by 10°.

The perceptual and postperceptual baseline conditions contained five heading directions (±20°, ±10°, and 0°). Each heading direction was repeated 20 times, so there were 100 trials. The perceptual and postperceptual load conditions contained 2 relative headings (±10°) × 5 heading directions (±20°, ±10°, 0°), a total of 10 combinations. Each combination was repeated 20 times, so there were 200 trials. All trials were randomly presented in each condition. The conducting sequences of the four conditions (i.e., blocks) were counterbalanced among participants. Before starting the experiment, participants were given 20 practice trials randomly selected from the block of the postperceptual baseline condition. The whole experiment lasted for about 35 min.

Data analysis

The data analysis methods were similar to Experiment 1, except that in the perceptual load and postperceptual load conditions, the relative heading (RH) between the previous first and current heading stimuli included two levels: ±10° (i.e., RH = ±10°). We calculated the slope by using the difference in the heading error or residual heading error between the two relative headings divided by the differences between the two relative headings, given as

\[ s_{SD} = \frac{HE_{10°} - HE_{-10°}}{(RH_{10°} - RH_{-10°})}, \]  \tag{5}

\[ s_{SD} = \frac{RHE_{10°} - RHE_{-10°}}{(RH_{10°} - RH_{-10°})}, \]  \tag{6}

where \( HE_{10°} \) (\( HE_{-10°} \)) means the heading error when the relative heading is 10° (−10°); \( RHE_{10°} \) (\( RHE_{-10°} \)) means the relative heading error when the relative heading is 10° (−10°). \( RH_{10°} \) (\( RH_{-10°} \)) means the relative heading is 10° (−10°).

Results

Experiment 1 and the current experiment showed similar result patterns about the center biases and serial dependence before ruling out the center bias. Please see Appendix Figures E1 and E2 for the related results.
To shorten the contents, we mainly reported the serial dependence after ruling out center bias.

**Figure 5** plots the results of serial dependence after ruling out center bias. It clearly shows that the result patterns were similar to **Experiment 1**. Specifically, the current heading perception was biased toward the first previous heading, meaning an attractive serial dependence is in heading perception. One-sample  test showed that the slopes ($s_{SD}$ or $s'_{SD}$) were all significantly larger than 0 ($t(19) = 3.53, p < 0.0022, \text{Cohen’s} \ d > 1.12$). However, the $s_{SD}$ and $s'_{SD}$ significantly decreased in the second and third previous headings. One-sample  test showed that neither $s_{SD}$ nor $s'_{SD}$ was significantly different from 0 ($t\!(9) < 1.52, p > 0.14, \text{Cohen’s} \ d < 0.48$). These results suggested that the serial dependence occurred within trial and disappeared between trials after ruling out the center bias. Additionally, the significant serial dependence in the perceptual condition suggested that the serial dependence occurred at the perceptual stage.

Paired samples  test showed that the $s_{SD}$ of the perceptual condition was significantly smaller than the $s_{SD}$ and $s'_{SD}$ of the postperceptual condition ($t(19) = -2.46, p = 0.024, \text{Cohen’s} \ d = 0.61$; $t(19) = -2.90, p = 0.0092, \text{Cohen’s} \ d = 0.80$), suggesting that the serial dependence occurred at the perceptual stage. The difference was not significant between the $s_{SD}$ and $s'_{SD}$ of the postperceptual condition ($t(19) = -0.12, p = 0.91, \text{Cohen’s} \ d = 0.0034$), suggesting that the previously perceived heading did not cause a stronger serial dependence than the previous actual heading.

**Discussion**

In this experiment, we found an attractive serial dependence in heading perception, consistent with **Experiment 1**. Importantly, using one number-adding task to inhibit participants from consciously noticing the heading direction in the perceptual condition, we found that the attractive serial dependence still existed, suggesting that the attractive serial dependence occurred at the perceptual stage.

The results also showed that a stronger attractive serial dependence was in the postperceptual condition than in the perceptual condition, suggesting that the attractive serial dependence also occurred at the postperceptual stage, inconsistent with the proposal that heading perception from optic flow was perceptual (Xing & Saunders, 2016).

Moreover, like in **Experiment 1**, the perceived heading of the previous stimuli did not cause a stronger serial dependence than the actual heading of the previous stimuli, suggesting that the decision-making stage might not be involved in the serial dependence in heading perception.

**Experiment 3: Heading perception is consistent with an ideal observer model**

Previous studies have shown a center bias in heading perception (D’Avossa & Kersten, 1996; Sun et al., 2020; Xing & Saunders, 2016; Warren & Saunders, 1995), consistent with an ideal observer model in which the straight-ahead direction works as a prior. When the reliability of the heading stimuli decreased, the center bias in heading perception became stronger (Sun et al., 2020; Xing & Saunders, 2016). Moreover, Sun et al. (2020) found that apart from center bias, a repulsive serial dependence was in heading perception, meaning that the perceived heading was biased away from the previously seen heading. They also found that the size of the repulsive serial dependence increased with the decrease of the reliability of heading stimuli, consistent with an ideal observer model in which the previous heading worked as a prior.

Two experiments in our current study revealed both attractive serial dependence and center bias existed in heading perception. In this experiment, we manipulated the reliability of heading stimuli by varying the dot density of heading stimuli to examine whether the heading perception from optic flow was consistent with an ideal observer model in which the straight-ahead direction and the previous heading served as priors. In other words, we aimed to investigate whether observers would optimally combine the information of straight-ahead direction, the previous headings, and the current heading to estimate their headings.

**Methods**

**Participants**

Eighteen participants (7 males and 11 females; age: 19–24 years) were enrolled from Zhejiang Normal University. They were with correct-to-normal vision and naive to the purpose of the experiment. The experiment was approved by the Scientific and Ethical Review Committee in the Department of Psychology of Zhejiang Normal University.

**Stimuli and apparatus**

The stimuli and apparatus were similar to **Experiment 1**, except that the heading stimuli consisted of 45, 90, or 135 dots, and headings were selected from $\pm 10^\circ$, $\pm 20^\circ$, and $\pm 30^\circ$. 
Figure 5. Results of serial dependence after ruling out center bias in Experiment 2. Panels (a) and (c) are the results of the perceptual condition, in which two heading stimuli were sequentially presented, and participants were only asked to judge the heading of the first stimulus. Panels (b) and (d) correspond to the postperceptual condition, in which participants were asked to judge the second heading after their response to the first heading. As a result, participants would initiatively remember the heading direction of the first stimulus in each trial of the postperceptual condition. In contrast, the process of the heading direction of the first stimulus in the perceptual condition would be inhibited by the integer-adding task. If the slopes of the linear fitting were significantly different, the postperceptual stage was involved in serial dependence of the heading perception. In (a) and (b), the x-axis is the relative heading, meaning the difference in the actual heading between the nth (n = 1, 2, etc.) previous and current headings. In (c) and (d), the x-axis
is the perceived relative heading, meaning the difference between the perceived heading of the \( n \)th previous heading stimulus and the actual heading of the current heading stimulus. The \( y \)-axis was the residual heading error that was the difference in the perceived heading between the perceptual (or postperceptual) and the baseline condition. “Left” and “Right” on the \( x \)-axis mean that the \( n \)th previous heading stimulus’s perceived heading was left or right of the current heading stimulus’s actual heading. “Left” and “Right” on the \( y \)-axis mean that the perceived heading was left or right of the perceived heading of baseline condition. Each circle represents the mean heading error averaged across 20 participants; the error bar represents the standard error across 20 participants. The horizontal dashed line represents no serial dependence in the heading perception. The solid line shows the best linear fitting result. The small panel on the top-right corner shows the averaged slope (diamond marker) and the slopes of 18 participants (light color dots). * \( p < 0.05; ** \( p < 0.01; *** \( p < 0.001.

Procedure

The experimental procedures were similar to Experiment 1, except participants were asked to finish four blocks of trials. Each block corresponded to one condition: 45-dot baseline, 135-dot baseline, 45-dot perceptual, and 135-dot perceptual conditions. The trial procedures of the former two conditions were similar to the baseline condition in Experiment 1 (left panel in Figure 1c), except that the heading stimulus consisted of 45 and 135 dots. The trial procedures of the latter two conditions were similar to the perceptual condition in Experiment 1 (middle panel in Figure 1c), except the first heading stimulus consisted of 90 dots and the second heading stimulus consisted of 45 and 135 dots.

Blocks 1 and 2 included two conditions. Each condition corresponded to one heading (−20° or 20°) and was repeated 30 times in each block. A total of 60 trials were included. Blocks 3 and 4 included 2 headings (±20°) × 2 relative headings (±10°), a total of four combinations. Each combination was repeated 15 times. A total of 60 trials were included. The sequences of the four blocks were counterbalanced among participants. Before the start of the experiment, participants were given 10 practice trials. The practice trial procedure was similar to Block 1, but the heading was randomly selected from ±10° and ±20°. The whole experiment lasted for about 30 min.

Data analysis

To evaluate center biases in different heading eccentricity, we used 1 minus the ratio between the perceived heading (\( PH \)) and the actual heading (\( AH \)), given as

\[
CB = 1 - \frac{PH}{AH}, \quad (7)
\]

where \( CB \) was the size of the center bias. If \( CB \) was significantly larger than 0, then a center bias was in heading perception. The larger the \( CB \), the stronger the center bias.

The data analysis method about the serial dependence was the same as in Experiment 1.

Ideal observer model

To examine whether the heading performance was the result of optimal combination of straight-ahead direction, currently presented heading, and the previously seen headings, we developed an ideal observer model, which was stated as

\[
P(\theta_C|M, \theta_P, S = 0) \propto P(M|\theta_C, \theta_P, S = 0)
\]

in which

\[
P(M|\theta_C, \theta_P, S = 0) = P(M|\theta_C, S = 0) \prod_i^n P(\theta_{C,i}|\theta_{P,i}, S = 0),
\]

where \( \theta_C \) means the heading of current trials, \( \theta_{P,i} \) means the heading of previous \( i \)th trials (\( i = 1, 2, \) etc.), \( M \) is the perceived heading of the current trial, and \( S \) is straight-ahead direction (0°). Note that, \( \theta_c \), \( \theta_{p,i} \), and \( S \) are independent. Equation 8 means that the posterior probability of a particular currently presented heading (\( \theta_C \)) given a particular sensory measurement (\( M \)) and straight direction (\( S = 0 \)) is proportional to the product of the likelihood of that measurement given a current heading (\( \theta_C \)), previous headings (\( \theta_P \)), and straight-ahead direction (\( S \)) and the prior probability of that measurement given the straight-ahead direction (\( S \)) and a serial of previous headings (\( \theta_{P,i} \)). When preheading was absent (i.e., baseline conditions), \( P(\theta_C|\theta_P, S = 0) = P(\theta_C|S = 0) = P(M|\theta_C, \theta_P, S = 0) = P(M|\theta_C, S = 0)\). So Equation 8 could be expressed as

\[
P(\theta_C|M, S = 0) \propto P(M|\theta_C, S = 0)P(\theta_C|S = 0).
\]

We proposed that the distributions of priors and likelihood were consistent with Von-Mises probability distributions:

\[
P(M|S) = e^{k_S \times \cos(M/S - \pi/180)} - 1, \quad \text{centered at } S = 0^\circ;
\]

\[
P(M|\theta_{P,i}) = e^{k_P \times \cos(M - \theta_{P,i}/180 - \pi)} - 1, \quad \text{centered at } \theta_{P,i} = \pm 10, \pm 20, \text{ or } \pm 30^\circ;
\]
\[ P(M|\theta_C) = e^{k_c \times \cos\left(\frac{\theta_C - \theta_{P,i,j}}{\varepsilon}\right) - 1}, \]

centered at
\[ \theta_C = \pm 20^\circ; \]

\[ S, \theta_P, \text{and} \theta_C \text{are constants.} \]

\[ M \text{is the mean perceived headings across 18 participants in different conditions.} \]

\[ k_C, k_P, \text{and} k_S \text{are free parameters that decided the width of the Von-Mises probability distributions.} \]

With the model, we first examined whether the optimal combination happened within trial—specifically, in the baseline condition, whether observers optimally combined the current heading \( P(M|\theta_C) \) and the straight-ahead direction \( P(\theta_C|S) \) to perceive heading and, in the perceptual condition, whether observers optimally combined the current heading, the straight-ahead direction, and the first previous heading \( \theta_{P,i,j} = -10 \) or \( -30 \) \((10 \text{ or} 30)\)° when the current heading was \(-20^\circ \) \((20)\)° that were in the same trial with the current heading.

Markov chain Monte Carlo (MCMC) sampling was used to estimate the parameters (i.e., \( k_C, k_P, \text{and} k_S \)). We used a 1,000,000 iterations as a burn-in period. Before starting the iteration, we randomly selected starting point values for \( k_C, k_P, \) and \( k_S \). For example, in our codes, \( k_C = [3, 3] \), corresponding to 45 and 135 dots in the flow field, and \( k_P = [3, 3] \), corresponding to \( \pm 30^\circ \) and \( \pm 10^\circ \) preheadings, \( k_S = 1 \). The start-point values did not affect the final results. From the second iteration, we added a random number \( \Delta \) selected from the standard normal distribution to the parameter values of preiteration. We compared the log-likelihood posterior \( LLP_c \) of the current iteration with the \( LLP_{c-1} \) of the pre–first iteration \( (c \text{ is the index of iteration}) \). For each dot number condition, each participant’s \( LLP' \) was given by

\[ LLP' = \sum_{i}^{2} \sum_{j}^{3} \log \left( P(M|\theta_C,S = 0, \theta_{P,i,j}) \right) \]
\[ + \log \left( P(\theta_C|S = 0, \theta_{P,i,j}) \right), \]

where \( \theta_{P,i,j} \) indicates two current headings \((\pm 20^\circ); i,j \) indicates three preheading conditions under one current heading \((e.g., i = 1, \text{meaning that the current heading is} \ -20^\circ); \) and the corresponding preheading conditions include three cases \((j = 1, 2, 3): -10^\circ, -30^\circ, \text{and no preheading conditions}) \.

We then summarized the \( LLP' \) of 18 participants and two dot-number conditions, given by

\[ LLP = \sum_{s}^{18} \sum_{k}^{2} LLP'_{s,k}, \]

in which, \( s \) represents the \( s \)th participants, and \( k \) represents the \( k \)th dot-number condition. If the \( LLP'_{c} \) of the current iteration was larger than the \( LLP'_{c-1} \) of the pre–first iteration, the parameter values of the current iteration were kept; if not, one random number \( (\varepsilon) \) was generated. If \( \varepsilon > 0.5 \), then the parameter values of the current iteration were kept; if \( \varepsilon \leq 0.5 \), the parameter values of the current iteration were equal to the parameter values of the preiteration. The same procedure was repeated a million times. The final values of \( k_C, k_P, \) and \( k_S \) were the mean of the 18,000 iterations selected from the 100,001st iteration to the end with step \( 50.3^\circ \).

If the 95% confidence intervals (CIs) of the participants’ performances were overlapped with the CIs of the predicted perceived headings of the ideal observer model, then the heading perception from optic flow was consistent with an ideal observer model, suggesting that observers could optimally combine the straight-ahead direction, previously seen heading, and currently presented heading to perceived heading.

The above procedure was also applied to examine whether the optimal combination happened within and between trials—specifically, in the baseline condition, whether observers optimally combined the straight-ahead direction and the current heading with the previous heading presented in the previous trials and, in the perceptual condition, whether observers optimally combined the straight-ahead direction, the current heading, and the previous heading presented in the same trial with the previous heading presented in the previous trial. The operations were similar to the above model for the within trials, except that in Equation 9, for each actual heading, \( j = 1, 2, ..., 6 \), that is, the combination of three within-trial preheadings \((10^\circ, 30^\circ, \text{and no preheading}) \) and two between-trial preheadings \((\pm 20^\circ) \).

Results and discussion

Behavior results

Figure 6 plots the size of center bias (CB) against the actual heading. It clearly shows that the sizes of the center bias are larger than 0 in all conditions supported by sample \( t \) tests \((ts(17) > 2.97, ps < 0.0087, \text{Cohen’s} \ d > 0.99) \), suggesting a center bias in heading perception from optic flow. Additionally, it also shows that the sizes of the center bias are generally larger in 45-dot condition than in 135-dot condition. One 2 conditions \(( \text{baseline vs. perceptual}) \times 2 \text{ dot numbers (45 vs. 135)} \) \times 2 \text{ actual headings (±20°)} \) repeated-measures ANOVA showed that the main effect of dot numbers was significant \((F(1,17) = 9.20, p < 0.001, \eta^2 = 0.35) \). Specifically, the size of the center bias of 45 dots \( (\text{black dots}, M \pm SE: 0.23 \pm 0.025) \) was larger than that of 135 dots \( (\text{blue dots}, 0.16 \pm 0.029) \). The interaction effect between conditions and actual headings was also significant \((F(1,17) = 5.80, p = 0.028, \eta^2 = 0.25) \).
other factors’ main effects and interaction effects were not significant ($p_s > 0.85$). The results suggested that the size of the center bias increased with the decrease of the dot number, indicating that observers relied more on the straight-ahead direction to perceive their heading as the reliability of heading stimuli decreased. This was consistent with an ideal model in which the straight-ahead direction worked as the prior.

The center bias was analyzed without ruling out the serial dependence. We, therefore, examined the effects of dot density on the serial dependence without ruling out the center bias. Figures 7a–d plot the heading error against the relative heading. The heading error was the difference between the perceived and actual headings of current stimuli. The relative heading was the difference in the actual heading between the nth ($n = 1, 2, 3,$ etc.) previous and current stimuli. All figures show when the previous heading is left (right) to the current heading, the perceived heading is biased toward the left (right) side of the actual heading, indicating an attractive serial dependence in heading perception. One-sample t test showed that all slopes ($s_{SD}$) were significantly larger than 0 ($t_{s(17)} > 2.52, ps < 0.022$, Cohen’s $d_S > 0.84$), suggesting an attractive serial dependence in all conditions.

Figure 7e plots the size of the serial dependence ($s_r$) against different previous headings in the baseline condition. In the baseline conditions, the dot numbers of the previous and current stimuli were the same. One 2 previous headings (first vs. second) × 2 dot numbers (45 vs. 135) repeated-measures ANOVA showed that the main effects of dot numbers were significant ($F(1, 17) = 6.62, p = 0.020$, $\eta^2 = 0.28$). Specifically, the $s_r$ of 45 dots ($M \pm SE: 0.14 \pm 0.018$) was larger than that of 135 dots ($0.098 \pm 0.017$), suggesting that the size of the serial dependence increased, with the decrease of the dot number indicating that observers relied more on previous headings as the reliability of current heading decreased. Neither the main effects of previous headings nor their interaction effect with dot numbers were significant ($F_s < 1, ps > 0.36$, $\eta^2_s < 0.048$).

The above result pattern was also observed in the perceptual conditions (Figure 7f). In the perceptual conditions, the dot numbers of the first and third previous stimuli were 90, different from current stimuli (45 or 135). In contrast, the dot number of the second previous stimuli was 90, same as the current stimuli. One 2 previous headings (first vs. third) × 2 dot numbers (45 vs. 135) repeated-measures ANOVA showed that the main effects of dot numbers were significant ($F(1, 17) = 6.25, p = 0.023$, $\eta^2 = 0.27$). Specifically, the $s_r$ of 45 dots ($M \pm SE: 0.14 \pm 0.039$) was larger than that of 135 dots ($0.098 \pm 0.013$). Neither the main effects of previous headings nor their interaction effect with dot numbers were significant ($F_s < 1, ps > 0.36$, $\eta^2_s < 0.048$). Paired sample t test showed that the $s_{SD}$ of 45 dots was significantly larger than that of 135 dots ($t_{17} = 3.11, p = 0.0064$, Cohen’s $d = 0.63$) in the second previous heading. These results suggested that the size of the serial dependence increased with the decrease of the dot density, indicating that observers relied more on previous headings as the reliability of current heading decreased.

Together, the current experiment well reproduced the finding of Experiments 1 and 2 that both the center bias and attractive serial dependence were in heading perception from optic flow. Importantly, both the sizes of the center bias and attractive serial dependence increased with the decrease of heading reliability, consistent with an ideal observer model.

**Ideal observer model**

Figure 8 shows the posterior distributions of heading directions ($P(\theta_C|M)$) predicted by the ideal observer model. Panels (a), (d), and (e) show the result of the ideal observer model, the priors of which do not include the between-trial preheadings; other panels show the result of the ideal observer model, the priors of which include the between-trial preheadings. Panels (a), (b), and (c) show the result of the ideal observer model, the priors of which do not include the within-trial preheading; other panels show the result of the ideal observer model, the priors of which include the within-trial preheading. The black and blue markers and lines correspond to 45- and 135-dot conditions.
Figure 7. (a–d) Results of the serial dependence without ruling out center bias in the 45- and 135-dot baseline and perceptual conditions. The x-axis was the relative heading that was the difference in the actual heading between the nth \( (n = 1, 2, \text{etc.}) \) previous and current stimuli. “Left” and “Right” on the x-axis mean that the nth previous heading stimulus’s actual heading was left or right of the current heading stimulus’s actual heading. The y-axis was the heading error that was the difference in the perceived heading and actual heading of the current heading stimulus. “Left” and “Right” on the y-axis mean that the perceived heading of the current heading stimulus was left or right of the actual heading. Each circle represents the mean heading error averaged across 18 participants; the error bar represents the standard error across 18 participants. The horizontal dashed line represents no serial dependence in the heading perception. Panels (e) and (f) plot the size of serial dependence \( (s) \) against nth \( (n = 1, 2, 3) \) previous headings. Gray and blue bars correspond to 45- and 135-dot conditions. *0.01 < \( p < 0.05 \); **0.001 < \( p < 0.01 \); ***\( p < 0.001 \).

The figure clearly shows that the participants’ perceived headings (diamond markers) are well covered by the posterior distribution. The 95% CIs of the participants’ perceived headings and the posterior distributions were very close (see Table 1 for the descriptive statistics), suggesting that the ideal observer model can well predict the performance of the heading perception from optic flow.

As shown in Figure 8a, when no heading stimulus was presented before the current heading (no preheading condition), the means of the posterior distributions were biased toward the straight-ahead direction \( (0^\circ) \), showing a center bias in heading perception. Additionally, the mean of the posterior distribution of the 45-dot condition (black curve) was more biased toward the straight-ahead direction than...
Figure 8. Posterior distribution of heading direction predicted by the ideal observer model. Panels (a), (d), and (e) show the result of the ideal observer model, the priors of which do not include the between-trial preheading; other panels show the result of the ideal observer model, the priors of which include the between-trials preheadings. Panels (a), (b), and (c) show the result of the ideal observer model, the priors of which do not include the within-trial preheading; other panels show the result of the ideal observer model, the priors of which include the within-trial preheading. Black and blue markers, curves, and lines correspond to the 45- and 135-dot conditions. The diamond markers show 18 participants’ perceived headings; the filled circle markers show the mean perceived headings averaged across 18 participants. The solid lines indicate the predicted mean of the ideal observer model. The dashed vertical lines indicate the upper and lower bounds of the 95% confidence intervals (CIs) of the posterior distributions. The horizontal error bars show the 95% CI of 18 participants’ performances.

Table 1. Descriptive statistics of behavioral results and ideal observer model results.
the posterior distribution of 135-dot condition (blue curve), consistent with the participants’ performance. This suggested that the center bias size increased with the decrease of the optic flow reliability, indicating that the center bias in heading perception from optic flow was consistent with the Bayesian inference account that observers could optimally combine the current heading information and the straight-ahead direction to estimate their heading.

Compared with no preheading condition (Figure 8a), when a heading was presented before the current heading in the previous trial (Figures 8b and 8c) or in the same trial (Figures 8d and 8g), the means of the posterior distribution were evidently biased toward the preheading, consistent with the participants’ performance, and the biases were well captured by the ideal observer model that contained two priors: straight-ahead direction and the between-trial or within-trial preheading.

Additionally, when both between-trial and within-trial preheadings were presented (Figures 8e, 8f, 8h, and 8i), the perceived headings were, on average, slightly biased toward the between-trial preheading. The trend could also be captured by the ideal observer model that contained three priors: straight-ahead direction and the within- and between-trials preheadings. Together, the results suggested the serial dependence in heading perception was consistent with the Bayesian inference account that observers could optimally combine the current heading information, the straight-ahead direction, and the previously seen headings to estimate their heading.

**General discussion**

Combining the three experiments, we have found an attractive serial dependence in heading perception from optic flow, and the serial dependence occurs at both the perceptual and postperceptual stages. Importantly, an ideal observer model, in which the straight-ahead direction and previously seen headings serve as priors, can well predict participants’ perceived headings. This result suggests that observers can optimally combine the information of straight-ahead direction, previously seen headings, and currently presented headings to estimate their headings.

Previous studies generally examined serial dependence without ruling out other effects first (e.g., Bae & Luck, 2020; Cicchini, Mikellidou, & Burr, 2017, 2018; Fischer & Whitney, 2014; Fritsche, Mostert, & de Lange, 2017). For example, a central tendency was generally observed in color perception. That is, the current perceived color was biased toward the mean of the previous color distribution (Olkkonen & Allred, 2014; Olkkonen, McCarthy, & Allred, 2014). Bae and Luck (2020) found an attractive serial dependence in color perception without ruling out central tendency. Similarly, without ruling out center bias, we found an attractive serial dependence in heading perception (also see Sun et al., 2020), consistent with the serial dependence studies with other features.

The current study revealed an attractive serial dependence in heading perception after ruling out center bias, different from the repulsive serial dependence revealed by Sun et al. (2020). Sun and his collaborators fitted the perceived heading as a linear function of heading eccentricity and used the slope of the linear function to evaluate the size of the center bias. That is, the size of center bias was constant along with the heading eccentricity. However, previous studies have proposed that the center bias in heading perception is consistent with a Bayesian inference account in which the straight-ahead direction works as the prior, which has been demonstrated by our ideal observer model in the current study. According to Bayesian inference theory (Bernardo & Smith, 1994; Jaynes, 1986; MacKay, 2003), the visual system will rely more on the forward motion direction (straight-ahead) as the reliability of optic flow decreases. Crowell and Banks (1993) have revealed that the reliability of optic flow decreases with the increase of heading eccentricity (also see Appendix A). Therefore, the size of the center bias increases with the heading eccentricity. The linear function adopted by Sun et al. (2020) leads to the overestimation of center bias for the central headings and the underestimation of the peripheral headings (see Appendix B). The residual heading error—the difference between the perceived heading and the predicted perceived heading—might be from the estimation loss of center bias instead of serial dependence. In the current study, we calculated the differences in the perceived heading of the current heading between the preheading presented and absent conditions, which could solve the problem caused by the inaccurate estimates of center bias and accurately reveal the effects of the previously seen heading on the current heading perception. With this method, an attractive serial dependence was revealed in the heading perception from optic flow.

Apart from the different serial dependence effects between the current study and Sun et al. (2020), the current study also found that the heading presented in the previous trial (i.e., between-trial heading) did not affect the heading perception of the current trial in the perceptual and postperceptual conditions after ruling out center bias. However, Sun et al. (2020) found that between-trial headings affected the current heading perception after ruling out center bias. The different findings can be due to the different experimental designs. Specifically, in Sun et al. (2020), each trial contained only one heading stimulus. In contrast, in the current study, two headings were sequentially presented in each trial, meaning that one heading was between the previous and current headings. The extra heading might eliminate or reduce the representation of the
between-trial heading in our brain. As a result, the linear regression analysis did not find an attractive serial dependence across sequential trials in the perceptual and postperceptual conditions.

The current study also showed that the perceived headings were well predicted by an ideal observer model that contained multiple priors: straight-ahead direction and previously seen heading. This finding provided direct evidence for the belief that heading perception from optic flow could be potentially explained by Bayesian frameworks (Sun et al., 2020; Xing & Saunders, 2016). However, these previous studies did not develop computational models to quantitively test their theories. Furthermore, our findings enabled the ideal observer model to have more degrees of freedom to combine three or more types of previous information together to predict behaviors. The ideal observer model used in previous studies contained only two types of information (for review, see Knill & Pouget, 2004; Landy, Banks, & Knill, 2011), such as visual and auditory information (Battaglia, Jacobs, & Aslin, 2003), form and motion (Kuai et al., 2020; Niehorster, Cheng, & Li, 2010), vestibular and visual information (Chen, DeAngelis, & Angelaki, 2011; Fetsch et al., 2009; Gu et al., 2016), and previous and current orientations (Cicchini et al., 2018).

Another important finding was that the serial dependence in heading perception occurred at the perceptual and postperceptual stages. Previous serial dependence studies initially found that the serial dependence occurred only at the perceptual stage (e.g., Cicchini et al., 2017; Fischer & Whitney, 2014; Manassi, Liberman, Kosovicheva, Zhang, & Whitney, 2018) or at the postperceptual stages (e.g., Bliss, Sun, & D’Esposito, 2017; Ceylan, Herzog, & Pascucci, 2021; Fritsche, Mostert, & de Lange, 2017; Pascucci et al., 2019). Recently, some studies have revealed that serial dependence occurs at both stages (e.g., Fornaciaci & Park, 2020). The current finding provides further evidence for the idea of two-stage involvement. Additionally, to reveal the involvement of the postperceptual stage in the serial dependence, we adopted the dual-task paradigm that was popular in the research area of working memory (Baddeley, 1992) and found that it worked. The dual-task paradigm can be an effective method for further serial dependence studies.

In summary, the current study found that not only center bias but also attractive serial dependence would jointly bias heading perception from optic flow. And the attractive serial dependence occurred at the perceptual and postperceptual (e.g., working memory) stages. Besides, both the center bias and the attractive serial dependence can be well predicted by an ideal observer model that contains multiple priors: straight-ahead direction and previously seen headings, suggesting that observers can optimally combine the straight-ahead direction and previous and current headings to estimate their heading. Together, the current study revealed the postperceptual mechanism of heading perception from optic flow, different from the idea that heading perception from optic flow is purely perceptual (Xing & Saunders, 2016), and provided direct evidence for the claim that heading perception is a performance-optimizing Bayesian process (Crowell & Banks, 1996; Fetsch et al., 2009).

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Footnotes

1 In one ongoing project, we tested the discrimination thresholds of different heading eccentricities. The results showed the discrimination threshold increased with the increase of heading eccentricity (see Appendix A), reproducing the results of Crowell and Banks (1993).

2 To test whether the perceived heading was linearly or nonlinearly increased with the heading eccentricity, we conducted one experiment in one ongoing project. The experimental methods were similar to Sun et al. (2020). The results showed that the prediction performance of a cubic function was significantly better than that of the linear function (see Appendix B).

3 We also tested the final results of other steps (e.g., 100, 1,000, 2,000) and found that the step did not affect the final results (see Appendix C).

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### Appendix A

In this experiment, six participants were enrolled. The stimuli (30.8° H × 30.8° V) were generated by simulating observers translating at 1.5 m/s in a 3D dot-cloud (12 dots, depth range: 0.3–1.0 m). The simulated heading directions were randomly selected from five ranges: [−14.5°, −7.5°], [−9°, −1.5°], [−3.5°, 3.5°], [1.5°, 9°], [7.5°, 14.5°]. Positive and negative values indicated the heading was right or left to the display center, respectively. The heading directions changed with a step of 0.7°. The centers of the ranges, i.e., −11°, −5°, 0°, 5°, 11°, were the target heading directions. In each trial, two 500-ms optic flow stimuli were sequentially presented. The heading of one optic flow stimulus was randomly selected from the above five target headings; the heading of the other stimulus was selected from the target heading’s corresponding range. Participants were asked to judge the heading of the 2nd one was left or right to the heading of the 1st one. We fitted the proportion of rightward responses as a psychometric function of the actual heading. The standard deviation (σ) of the psychometric function reflected the heading discrimination threshold. A larger standard deviation indicated the lower reliability of optic flow stimuli. The results showed that the standard deviation increased with the heading eccentricity (Figure A1), consistent with the Crowell and Banks (1993).

![Figure A1](https://example.com/figureA1.png)

Figure A1. The proportion of rightward responses against the actual heading (i.e., heading eccentricity). The dots represent the mean proportion of rightward responses averaged across 6 participants; error bars are the standard error across 6 participants.

### Appendix B

In this experiment, 14 participants were enrolled. The stimuli (30.8° H × 30.8° V) were generated by simulating observers translating at 1.5 m/s in a 3D dot-cloud (12 dots, depth range: 0.3–1.0 m). The simulated heading directions were randomly selected from five ranges: [−14.5°, −7.5°], [−9°, −1.5°], [−3.5°, 3.5°], [1.5°, 9°], [7.5°, 14.5°]. Positive and negative values indicated the heading was right or left to the display center, respectively. The heading directions changed with a step of 0.7°. The centers of the ranges, i.e., −11°, −5°, 0°, 5°, 11°, were the target heading directions. In each trial, two 500-ms optic flow stimuli were sequentially presented. The heading of one optic flow stimulus was randomly selected from the above five target headings; the heading of the other stimulus was selected from the target heading’s corresponding range. Participants were asked to judge the heading of the 2nd one was left or right to the heading of the 1st one. We fitted the proportion of rightward responses as a psychometric function of the actual heading. The standard deviation (σ) of the psychometric function reflected the heading discrimination threshold. A larger standard deviation indicated the lower reliability of optic flow stimuli. The results showed that the standard deviation increased with the heading eccentricity (Figure A1), consistent with the Crowell and Banks (1993).
Figure B1. Perceived heading against actual heading. The dots represent the mean perceived heading averaged across 14 participants; shaded error bars show the standard error across 14 participants. The solid lines plot the fitting results of linear function (left panel) and cubic function (right panel).

### Linear function
\[
H_p = S_C H_A + \text{error}
\]

### Cubic function
\[
H_p = a_C H_A^3 + S_C H_A + \text{error}
\]

### Function statistics

|               | Linear function | Cubic function |
|---------------|-----------------|----------------|
| Deviance      | 8.50            | -2.99          |
| \(\chi^2(df)\) | 3.92 (9)        | 2.32 (8)       |
| P             | 0.92            | 0.97           |

Table B1. Results of cubic and linear functions.

|                 | Step = 50 | Step = 100 | Step = 1000 | Step = 2000 |
|-----------------|-----------|------------|-------------|-------------|
|                 | 40.66     | 40.67      | 40.65       | 40.67       |
| Pre-heading (°) | 10        | 30         | 10          | 30          | 10          | 30          |
| \(k_P\)         | 8.37      | 43.19      | 8.38        | 43.21       | 8.27        | 43.55       | 8.24        | 42.92       |
| Dot number      | 45        | 135        | 135         | 45          | 135         | 45          | 135         |             |
| \(k_C\)         | 144.17    | 219.88     | 144.19      | 219.97      | 144.29      | 219.99      | 143.78      | 220.05      |
| No pre-heading  |           |            |             |             |             |             |             |             |
| Mean            | 15.64     | [8.65, 22.62] | 16.92 | [11.04, 22.78] |
| 95% CI          |           |             |             |             |             |             |             |             |
| Peripheral 10°-offset |       |            |             |             |             |             |             |             |
| Mean            | 16.26     | [9.42, 23.09] | 17.32 | [11.54, 23.10] |
| 95% CI          |           |             |             |             |             |             |             |             |
| Central 10°-offset |       |            |             |             |             |             |             |             |
| Mean            | 14.56     | [8.28, 20.84] | 15.93 | [10.48, 21.36] |
| 95% CI          |           |             |             |             |             |             |             |             |

Table C1. Descriptive statistics of ideal observer model results with different step size, e.g., 50, 100, 1000, and 2000.
In this experiment, 13 participants were enrolled. The stimuli (80° H × 80° V) were generated by simulating observers translating at 1 m/s in a 3D dot-cloud (90 dots, depth range: 0.2–5.0 m). The simulated headings were randomly selected from [−30°, 30°] with 7.5°-step. Positive and negative values indicated the heading was right or left to the display center, respectively. In each trial, a 500-ms optic flow stimulus was presented. After a while (e.g., 0s, 2s, 4s and 8s), participants then were asked to report their perceived heading by moving a mouse-controlled probe. One 4 delay time × 9 headings repeated measures ANOVA showed that the main effects of delay time was insignificant ($F(1.99, 23.83) = 1.48, p = 0.96, \eta^2 = 0.012$). The interaction between the two factor was significant ($F(7.54, 90.17) = 2.29, p = 0.96, \eta^2 = 0.031$). Further analysis showed that none of the main effects of delay was significant under each heading ($ps > 0.069$). The results suggested that the delay time had no effect on heading perception, indicating that working memory was not involved in heading perception.

### Appendix E

Figures E1a, E1b, E1d and E1e plot the perceived heading against the actual heading under the perceptual baseline, perceptual load, post-perceptual baseline and post-perceptual load conditions. Note that two heading stimuli were sequentially presented on each trial of the perceptual load and post-perceptual load conditions, hence Figures E1b and E1e show the results of the 2nd heading stimulus. The figures clearly shows that the perceived headings were systematically compressed towards the display center showing a center bias. The lines were the best fitting of Equation 1 and accounted for over 99.1% variance in the perceived heading. One sample $t$-test showed that the slopes of the four conditions were all significantly below 1 ($ts(19) < 4.45, ps < 0.001, Cohen’s dS > 1.41$), indicating a center bias in these conditions.

Figure E1f plots the perceived heading of the 1st heading stimuli against the actual heading in the post-perceptual load condition. It clearly shows that the perceived heading increases with the actual heading. The fitted line accounted for 99.2% of variance in the perceived heading. One sample $t$-test showed that the slope of the fitted line was significantly larger than 0 ($t(19) = 19.06, p < 0.001, Cohen’s d = 6.03$), indicating that participants followed the instruction to memorize the 1st heading stimuli’s heading direction in the post-perceptual load condition.

Figures E2a–E2d plot the heading error against the relative heading in the perceptual baseline, perceptual load, post-perceptual baseline, and post-perceptual load conditions. They show that in all conditions, when the previous heading is left to the current heading (i.e., relative heading was negative), the perceived heading was left to the actual heading (i.e., heading error was negative); vice versa. This suggests that the perceived heading is biased towards the previous heading indicating an attractive serial dependence in heading perception. Notethat the relative headings only included ±10° for the serial dependence of previous 1st heading in the perceptual load and post-perceptual load conditions, we calculated the slope with Equations 5 and 6 rather than fitted a linear function. For the conditions, we fitted the heading error as a linear function of the relative heading (Equation 2). The linear regression analysis showed that the fitted lines accounted for over 94.8% variance in the heading error. One sample $t$-test revealed that the slope ($ssd$) was significantly larger than 0 ($ts(19) > 3.53, ps < 0.0022, Cohen’s dS > 1.43$), indicating a significant serial dependence in heading perception and the SD could lasted for several seconds.
Figure E1. (a)–(b), (d)–(f) Center bias in Experiment 2. In each panel, the x-axis (y-axis) was the actual heading (perceived heading). “Left” and “Right” on the x-axis (y-axis) mean that the actual heading (perceived heading) is left or right to the display center (0°). Each circle represents the mean perceived heading averaged across 20 participants; the error bar represents the standard error across 20 participants. The horizontal dashed line represents the pure center bias meaning that participants always indicated the display center (0°) regardless of the actual heading. The diagonal dashed line represents the perfect performance meaning that participants accurately perceived the heading. The solid line shows the best linear fitting result. The small panel on the top-right corner shows the averaged slope (diamond marker) and the slopes of 20 participants (light color dots). (c) Accuracy of number comparison task in the perceptual baseline and perceptual load conditions. Error bar represents the standard deviation across 20 participants. *, $0.01 < p < 0.05$; **, $0.001 < p < 0.01$; ***, $p < 0.001$. 

\[ y = 0.81 \times 0.73, R^2 = 0.994 \]
\[ 95\% \text{ CI: Slope} \quad [0.710, 0.915] \]
\[ \text{intercept} \quad [-0.718, 2.180] \]

\[ y = 0.76 \times 1.04, R^2 = 0.992 \]
\[ 95\% \text{ CI: Slope} \quad [0.650, 0.863] \]
\[ \text{intercept} \quad [-0.466, 2.546] \]

\[ y = 0.85 \times 0.67, R^2 = 0.991 \]
\[ 95\% \text{ CI: Slope} \quad [0.715, 0.976] \]
\[ \text{intercept} \quad [-1.179, 2.520] \]

\[ y = 0.79 \times 0.94, R^2 = 0.999 \]
\[ 95\% \text{ CI: Slope} \quad [0.751, 0.831] \]
\[ \text{intercept} \quad [-0.368, 1.503] \]
Figure E2. Results of serial dependence before factoring out center bias in Experiment 2. The x-axis was the relative heading that was the difference in the actual heading between the previous $n^{th}$ ($n = 1, 2,$ etc.) and current stimuli. “Left” and “Right” on the x-axis mean that the previous $n^{th}$ heading stimulus’s actual heading was left or right to the current heading stimulus’s actual heading. The y-axis was the heading error that was the difference in the perceived heading and actual heading of the current heading stimulus. “Left” and “Right” on the x-axis mean that the previous $n^{th}$ heading stimulus’s actual heading was left or right to the current heading stimulus’s actual heading. “Left” and “Right” on the y-axis mean that the perceived heading of the current heading stimulus was left or right to the actual heading. Each circle represents the mean heading error averaged across 20 participants; the error bar represents the standard error across 20 participants. The horizontal dashed line represents no serial dependence in the heading perception. The solid line shows the best linear fitting result. The small panel on the top-right corner shows the averaged slope (diamond marker) and the slopes of 20 participants (light color dots). (a)–(d) show the results of the serial dependence in the perceptual baseline, perceptual load, post-perceptual baseline and post-perceptual load conditions. *, $0.01 < p < 0.05$; **, $0.001 < p < 0.01$; ***, $p < 0.001$. 

(a) Previous 1st heading
- HE: 0.10 RH: 0.70, $R^2$: 0.960
- 95% CI: $\pm$ 0.085
- error: [0.252, 1.146]

(b) Previous 2nd heading
- HE: 0.11 RH: 0.77, $R^2$: 0.974
- 95% CI: $\pm$ 0.095
- error: [0.378, 1.155]

(c) Previous 3rd heading
- HE: 0.12 RH: 1.12, $R^2$: 0.993
- 95% CI: $\pm$ 0.110
- error: [0.894, 1.132]

(d) Previous 4th heading
- HE: 0.09 RH: 0.77, $R^2$: 0.986
- 95% CI: $\pm$ 0.083
- error: [0.823, 1.323]