Attractive effects of previous form information on heading estimation from optic flow occur at perceptual stage

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Introduction

When moving in the environment, optic flow and form (e.g., motion streaks) information generally appear simultaneously. Previous studies have shown that observers can estimate their heading by integrating the simultaneously presented form and optic flow information. Recent work also found that the previously seen optic flow affected the current heading estimation. The current study conducted two experiments to explore whether and how the heading estimation from optic flow was affected by the previously seen form information. We found that the current heading estimates from optic flow were biased toward the location of the focus of expansion of the previously seen form stimulus, showing an attractive effect of the previous form. Additionally, the results revealed that the attractive effect of the previous form occurred at the perceptual stage rather than postperceptual stages (e.g., working memory). Our findings suggest that our visual system can integrate dynamic optic flow and static form information across the temporal domain to estimate our heading direction.

Accurately estimating self-motion direction (i.e., heading) is vital for the survival of people and animals. To make it, observers would integrate visual and nonvisual information (e.g., vestibular, proprioception). The visual information can be dynamic or static. The dynamic visual information refers to the global motion pattern projected on observers’ retina as observers move in the environment, named optic flow (Gibson, 1950). The static visual information means the global form structure of “motion streaks” arising through temporal integration of motion of environmental points beyond a single velocity field (Burr, 2000; Geisler, 1999). Both types of visual information share similar structures. For example, when observers move straight forward, both form and motion patterns are expansion and contain one focus of expansion (FoE). Previous studies have shown that observers can accurately estimate their heading within 1° to 2° error by locating the FoE in optic flow (e.g., Crowell & Banks, 1996; Li, Peli, & Warren, 2002; Warren, Morris, & Kalish, 1988).

Niehorster, Cheng, and Li (2010) found that observers could optimally integrate the simultaneously presented form and optic flow to estimate their heading...
direction. In one experimental condition, they showed participants Glass pattern stimuli consisting of 100 dot pairs. The motion of all dots simulated observers translating in different directions (red “+” in Figure 1a). Meanwhile, all dot pairs orientated to one position of the display, which generated a form FoE (blue “×” in Figure 1a) in each frame that was left or right to the heading direction from optic flow by 0°, 5°, or 10° (i.e., form FoE offset). Participants were asked to indicate their heading estimate in each trial by moving a mouse-controlled probe on a horizontal line after the stimulus disappeared. The results showed that the heading estimates were between the form FoE (oblique dashed line) and the heading from optic flow (horizontal dashed line) (blue line in Figure 1c). When one proportion of dot pairs was replaced with randomly oriented dot pairs (50% of dot pairs were randomized in Figure 1b), the heading estimates were biased more away from the form FoE and closer to the heading from optic flow (purple line in Figure 1c). The bias size increased with the decrease of dot-pair coherence, suggesting that observers relied more on optic flow information to estimate their heading when the reliability of the form information decreased, which is consistent with the Bayesian inference account (Bernardo & Smith, 1994; Cox, 1946; Jaynes, 1986; MacKay, 2003). Kuai, Chen, Xu, Li, Field, and Li (2020) later reproduced their findings. With functional magnetic resonance imaging (fMRI) techniques and multivariate pattern analysis (MVPA), they also found that the response patterns of the V3B/KO cortical area well matched the behavior performances, providing the neural basis for the optimal integration of form and flow information in heading estimation.

Sun, Zhang, Alais, and Li (2020) found that the previously seen headings could affect the current heading estimate from optic flow. Specifically, each trial started with an optic flow stimulus, followed by participants’ estimation using a mouse-controlled probe. The results showed that the current estimate from optic flow was biased toward the heading in the previous trial, showing an attractive effect of previous optic flow. Given that the heading estimates from optic flow were generally compressed towards the display center, showing a center bias effect (Li et al., 2002; Warren & Hannon, 1988; Warren & Kurtz, 1992; Warren & Saunders, 1995; Xing & Saunders, 2016; Sun et al., 2020), they fitted a linear function to estimate the error caused by center bias. Then, they eliminated the predicted error caused by center bias from the perceived error. The results showed that the current heading estimate was biased away from the previous heading, showing a repulsive effect of previous optic flow.

The effects of previously seen features on the current perception also have been observed in many other physical features, such as orientation (Ceylan, Herzog, & Pascucci, 2021; Cicchini, Mikellidou, & Burr, 2017; Cicchini, Mikellidou, & Burr, 2018; Fischer & Whitney, 2014; Fritsche, Mostert, & de Lange, 2017; Pascucci, Mancuso, Santandrea, Della Libera, Plomp, & Chelazzi, 2019; Samaha, Switzky, & Postle, 2019), spatial position (Bliss, Sun, & D’Esposito, 2017; Manassi, Liberman, Kosovicheva, Zhang, & Whitney, 2018), expression, identity, and attractiveness of faces (Kim, 2021; Liberman, Fischer, & Whitney, 2014; Taubert, Van der Berg, & Alais, 2016; Xia, Leib, & Whitney, 2016), and numerosity (Kim, Burr, Cicchini, & Alais, 2020; Fornaciai & Park, 2018). Additionally, recent work focused on the occurrence mechanism of the previous stimulus effect. That is, does the effect occur at the perceptual or postperceptual stages? Some studies showed that the effect was mainly perceptual...
different types of information across temporal domains. Exploring this question can improve our understanding of postperceptual process (e.g., working memory, decision-making) (Barbosa & Compte, 2020; Ceylan et al., 2021; Bliss, Sun, D’Esposito, 2017; Fritsche et al., 2017; Pascucci et al., 2019; Fornaciai & Park, 2020; Xu, Sun, Zhang, & Li, 2022).

Given the fact that form and motion information appear simultaneously in daily life and that Sun et al. (2020) have addressed the effect of previous form information on the current heading estimation from optic flow, we explored whether and how the previous form information affects the heading estimation from optic flow. Specifically, are the current heading estimates from optic flow biased toward or away from the previous form FoE? If the previous form information affects heading estimate from optic flow, does the effect occur at the perceptual or postperceptual stages? We conducted two experiments to answer these questions. Exploring this question can improve our understanding of the mechanisms underlying the integration of different types of information across temporal domains.

### Experiment 1: Attractive effects of the previous form information on heading estimation from optic flow

The current experiment explored whether and how previously seen form information affected the heading estimation from optic flow and whether the effects of the previous form occurred at the perceptual or postperceptual stages. The experiment included three experimental conditions: form-absent, form perceptual load, and form memory load conditions. On each trial of the form-absent condition, one optic flow stimulus was presented after a blank display, and participants were asked to reproduce their heading (Figure 3a). On each trial of the form perceptual load condition, one optic flow stimulus was presented after a form stimulus. The participants were asked to reproduce their heading from optic flow (Figure 3b). If there were significant differences in heading estimates between the two conditions, the heading estimation from optic flow could be affected by the previously presented form information. Since we only showed form information to participants and did not instruct them to view or memorize the form information (e.g., the position of form FoE), this result also indicated that the effects of the previous form could occur at the perceptual stage.

The procedure of the form memory load condition was similar to that of the perceptual load condition, except participants were asked to estimate the position of the form FoE by using a mouse-controlled probe after they reproduced the heading from optic flow (Figure 3c). To complete this task, they should keep the previous form FoE in their mind. Consequently, compared with the form perceptual load condition, the form information took more postperceptual resources in the form memory load condition. If there were significant differences in heading error between the perceptual and memory load conditions, then the effect of the previous form on the heading estimation from optic flow should occurred at postperceptual stage.

### Method

#### Participants

Sixty participants (20 males, 40 females; 18–26 years) were enrolled at Zhejiang Normal University. They were randomly divided into two groups of 30 participants each. All were naive to the experimental purposes and had normal or corrected-to-normal vision. The experiment was approved by the Scientific and Ethical Review Committee in the Department of Psychology of Zhejiang Normal University. The written consent form was obtained from each participant before participating in the experiment.

#### Stimuli and apparatus

Participants viewed two types of visual stimuli: optic flow and form stimuli. Optic flow (112° H × 80° V, Figure 2a) simulated observers translating in a three-dimensional (3D) dot-cloud at 1.5 m/s. The 3D dot-cloud consisted of 200 dots (diameter: 0.28°, luminance: 22.5 cd/cm²). Its depth range was from 0.2 m to 5 m. The simulated observers’ self-motion direction (i.e., heading, indicated by flow FoE) included ±6°, ±18°, and ±30°. The negative and positive values indicated that the heading was left or right to the display center (0°).

The form stimulus (112° H × 80° V, Figure 2b) consisted of 100 dot pairs (diameter: 0.28°, luminance: 22.5 cd/cm²). The distance between two dots in one pair was 1°. All dot pairs were oriented toward a location on the screen (i.e., the form FoE). The distance between the form FoE and the heading from optic flow (i.e., form FoE offset) included ±5°, ±15° and ±25°. The negative and positive values indicated that the form FoE was left or right to the heading from optic flow.

The experimental stimuli were programmed in MATLAB with PsychToolBox 3 and presented on a 27-inch ASUS monitor (resolution: 2560 × 1440 pixels; refresh rate: 60 Hz) with NVIDIA GeForce GTX 1660Ti graphics card.
Figure 2. Illustrations of stimuli used in the current study. (a) Optic flow stimulus. All dots were randomly positioned in a 3D space. The white dots illustrate the position of dots at the first frame of the display; the white lines (invisible in the experiment) illustrate the dots’ instantaneous motion speeds. The orientation indicates the motion direction; the length indicates the velocity. Yellow “+” indicates the heading direction (flow FoE). (b) Form stimulus. One hundred dot pairs were included. All dot pairs are oriented to one position of the display (form FoE), illustrated by the blue “x.”

Figure 3. Trial procedures of the (a) form-absent, (b) form perceptual load, and (c) form memory load conditions.

Procedure

Participants were in a light-excluded room. The distance between their heads and the computer display was 20 cm. Their heads were fixed with a chin rest. They viewed the stimuli with their right eye, reducing the conflict between motion parallax (indicating a 3D moving stimulus) and binocular parallax (indicating a flat two-dimensional display screen) depth cues. Participants were asked to fixate on the display center without any movement of head and body.

The current experiment included three conditions: form-absent, form perceptual load, and form memory load conditions. Each trial of form-absent condition (Figure 3a) started with a blue fixation dot, lasting for 500 ms. Then a 700-ms blank display was presented, followed by a 500-ms optic flow stimulus. After the optic flow display, participants were asked to move a mouse-controlled blue probe on a white horizontal line to indicate their heading estimate from optic flow. After they clicked the mouse, a 1200-ms blank display was presented. Then, next trial started. The trial procedure of form perceptual load condition (Figure 3b) was similar to that of form-absent condition, except that (1) a red fixation dot was first presented; (2) one 500-ms form stimulus and one 200-ms blank display replaced the first blank display in the form-absent condition. The trial procedure of form memory load condition...
was similar to that of form perceptual load condition, except the last 1200-ms blank display in perceptual condition was replaced with a 200-ms blank display and a response display. During the presentation of the response display, participants were asked to estimate the position of the form FoE by using a mouse-controlled blue probe on a white horizontal line (Figure 3c).

The current experiment included Experiment 1a and 1b. Participants of Group 1 completed Experiment 1a that contained form-absent and form perceptual load conditions. Participants of Group 2 completed Experiment 1b that contained form-absent and form memory load conditions. Each participants conducted a total of 672 trials (16 trials × 7 form FoE offsets [form-absent, ±5°, ±15°, and ±25°] × 6 headings [±6°, ±18°, and ±30°]). All trials are randomly presented. Each participant began with a practice of 20 trials to ensure that they understood the task and could perform it. Each sub-experiment lasted about 40 minutes.

**Data analysis**

We recorded the heading estimate of each trial and calculated the heading error meaning the difference between the heading estimate and the actual heading. To examine whether the previous form information affected the heading estimation from optic flow, one two-way (7 form FoE offsets × 6 headings) repeated-measures analysis of variance (ANOVA) and Newman-Keuls post hoc analysis were adopted on heading errors for Experiments 1a and 1b, respectively. If the previous form information affected heading estimation from optic flow, it was expected that (1) the main effect of form FoE offsets is significant; or (2) the interaction between form FoE offsets and headings is significant. Further Newman-Keuls post hoc analysis would show effects of form FoE offsets on heading estimation in different headings. Additionally, if the above significant results happened in perceptual load condition (Experiment 1a), then the effect of previous form information occurred at the perceptual stage.

In each sub-experiment, the form-absent condition served as the baseline. In Experiment 1a, we calculated the difference in heading error between one form FoE offsets and the form-absent condition, named residual heading errors. The residual heading errors were proposed to be originated from the perceptual stage. We also calculated residual heading errors in Experiment 1b, which were proposed to be originated from the perceptual and postperceptual stages. Then, one three-way (2 experiments × 6 form FoE offsets [±5°, ±15°, and ±25°] × 6 headings) repeated measures ANOVA analysis was adopted on residual heading errors. If the effect of previous form occurred at postperceptual stages, then it was expected that (1) the main effect of experiments was significant, or (2) the interaction between experiments and form FoE offsets was significant. The Newman-Keuls post hoc analysis would show that the effects of form FoE offsets on heading estimation varied in two experiments.

**Result and discussion**

To show result trends, we plotted the mean heading error averaged across 30 participants against the actual heading in form-absent, ±25° form FoE offset conditions in Figures 4a (Experiment 1a) and 4b (Experiment 1b). “Left” and “Right” on the x-axis mean the actual heading to the left or right of the display center (0°). “Left” and “Right” on the y-axis mean the heading estimate to the left or right to the actual heading. “Left” and “Right” on the legend mean the form FoE to the left or right of the heading from optic flow. Two figures clearly show that when the previous form FoE is left to the heading from optic flow (circles), the heading error is more left biased than the form-absent condition; vice versa. This suggests that the heading estimate from optic flow is biased towards the previous form FoE, showing an attractive effect, which is supported by our following statistical results.

A two-way (7 form FoE offsets × 6 headings) repeated measures ANOVA showed that in Experiment 1a, as expected, the main effect of form FoE offsets was significant (F(6, 174) = 12.77, p < 0.001, η² = 0.31). Newman-Keuls post hoc analysis showed that the heading errors of the −25°, −15° form FoE offsets (Mean ± standard error [SE]: −0.82 ± 0.92, 0.87 ± 0.93) were more left biased than the form-absent condition (−0.14 ± 0.90) (p = 0.035, p = 0.040); the heading errors of the 5°, 15°, 25° form FoE offsets (0.51 ± 0.89, 0.83 ± 0.93, 0.64 ± 0.94) were more right biased than the form-absent condition (p = 0.019, p = 0.002, p = 0.012). Additionally, the interaction between form FoE offsets and headings was significant (F(30, 870) = 1.62, p = 0.020, η² = 0.053). Newman-Keuls post hoc analysis (see white and blue bars in Figure 4c, Table 1 shows the descriptive statistics) showed that, on average, when the form FoE was to the left of the heading from optic flow, the perceived heading was biased toward the left side; vice versa. For example, when the actual heading was −30°, the degree of the right-biased heading error of 25° (6.01 ± 1.19) was significantly greater than that of −25° (3.80 ± 1.28) (p < 0.001); when the actual heading was 30°, the degree of the left-biased heading error of −25° (−6.14 ± 1.17) was greater than that of 15° (−4.08 ± 1.17) (p < 0.001). Together, these results suggest that the heading estimate from optic flow is biased toward the previous form FoE, meaning that the previous form attractively affects heading estimation from optic flow. Additionally, because in Experiment 1a the form stimulus was only presented on display and
Figure 4. Results of Experiment 1. (a–c) The mean heading error averaged across 30 participants against the actual heading for Experiments 1a and 1b. To make readers understand results clearly, we only plotted the results of form-absent condition, −25° and 25° form FoE offsets in panels a and b. “Left” and “Right” on the x-axis mean the actual heading to the left or right of the display center (0°). “Left” and “Right” on the y-axis mean the heading estimate is left or right to the actual heading. “Left” and “Right” on the legend mean that the form FoE is left or right to the heading from optic flow. Each dot or circle represents the mean heading error averaged across 30 participants. The error bar represents the standard error across 30 participants. (c) Detailed results in Experiment 1 including all conditions. The left y-axis (blue) serves for Experiment 1a and the upper part is the positive axis. The right y-axis (red) serves for Experiment 1b. The upper part is the negative axis. *, p < 0.05; **, p < 0.01; ***, p < 0.001. (d) Results of the form FoE reproduction task in the form memory load condition of Experiment 1b. “Left” and “Right” on the x-axis (y-axis) mean that the actual (perceived) form FoE is left or right to the display center (0°). Each dot represents the mean perceived form FoE averaged across 30 participants. The error bar represents the standard error averaged across 30 participants. (e) Residual heading error against the form FoE offset in Experiments 1a (blue) and 1b (red). Residual heading error means the difference in heading error between one form FoE offset (e.g., ±5°, ±15°, and ±25°) condition and the form-absent condition. Error bar indicates the standard error across 30 participants.

participants were not instructed to view or remember the information about the form stimulus, the attractive effect of previous form on heading estimation from optic flow could occur at the perceptual stage.

Gray and red bars in Figure 4c show the result patterns were similar to Experiment 1a, also revealing an attractive effect of the previous form (see Appendix for detailed results). Figure 4d clearly shows that even though the accuracy of form FoE perception was not very high, the perceived form FoE increased with the actual form FoE, suggesting that participants followed the instruction to remember the form FoE in Experiment 1b.

To explore whether the attractive form effect occurred at postperceptual stages (e.g., working memory), we calculated the residual heading errors of Experiments 1a and 1b. Figure 4e plots the mean residual heading error averaged across 30 participants against form FoE offsets. It shows an interaction effect between experiments and form FoE offsets. The difference in
### Table 1. Descriptive statistics of Experiment 1a.

| Actual heading | $-30^\circ$ | $-18^\circ$ | $-6^\circ$ | $6^\circ$ | $18^\circ$ | $30^\circ$ |
|----------------|------------|------------|------------|-----------|-----------|-----------|
| Form-absent    | Mean       | SE         | Mean       | SE        | Mean       | SE        | Mean       | SE         | Mean       | SE         |
|                | 5.88       | 1.19       | 1.70       | 0.84      | 0.45       | 0.70      | $-0.30$    | 0.68       | $-2.70$    | 0.85       | $-5.88$    | 1.12      |
| Form FoE offset| $-25^\circ$| 3.80       | 1.28       | 0.67       | 0.98       | 0.49       | 0.74       | $-1.10$    | 0.59       | $-2.65$    | 0.77       | $-6.14$    | 1.17      |
|                | $-15^\circ$| 4.25       | 1.10       | 0.89       | 0.92       | $-0.31$    | 0.75       | $-1.72$    | 0.79       | $-2.13$    | 0.83       | $-6.19$    | 1.19      |
|                | $-5^\circ$ | 4.30       | 1.20       | 0.43       | 0.87       | 0.69       | 0.64       | $-0.42$    | 0.61       | $-1.90$    | 0.92       | $-4.84$    | 1.18      |
|                | $5^\circ$  | 5.44       | 1.19       | 2.26       | 0.78       | 1.16       | 0.71       | $-0.48$    | 0.59       | $-1.11$    | 0.90       | $-4.24$    | 1.17      |
|                | $15^\circ$ | 5.58       | 1.19       | 2.75       | 0.96       | 1.36       | 0.73       | $0.28$     | 0.67       | $-0.94$    | 0.90       | $-4.08$    | 1.17      |
|                | $25^\circ$ | 6.01       | 1.19       | 2.48       | 1.07       | 1.95       | 0.78       | $-0.19$    | 0.70       | $-1.25$    | 0.76       | $-5.14$    | 1.16      |

### Table 2. Descriptive statistics of Experiment 1b.

| Actual heading | $-30^\circ$ | $-18^\circ$ | $-6^\circ$ | $6^\circ$ | $18^\circ$ | $30^\circ$ |
|----------------|------------|------------|------------|-----------|-----------|-----------|
| Form-absent    | Mean       | SE         | Mean       | SE        | Mean       | SE        | Mean       | SE         | Mean       | SE         |
|                | 5.54       | 1.09       | 2.46       | 0.99      | 0.72       | 0.60      | $-0.88$    | 0.60       | $-1.68$    | 1.05       | $-4.75$    | 1.24      |
| Form FoE offset| $-25^\circ$| 5.93       | 1.53       | 2.03       | 1.07      | $-0.29$    | 1.00       | $-4.00$    | 1.32       | $-5.63$    | 1.40       | $-6.64$    | 1.44      |
|                | $-15^\circ$| 5.11       | 1.30       | 1.65       | 1.00      | 0.03       | 0.83       | $-2.82$    | 0.90       | $-3.62$    | 1.08       | $-5.35$    | 1.27      |
|                | $-5^\circ$ | 5.10       | 1.22       | 2.27       | 0.93      | 0.19       | 0.78       | $-1.47$    | 0.67       | $-2.03$    | 0.97       | $-4.71$    | 1.11      |
|                | $5^\circ$  | 5.37       | 1.24       | 2.87       | 0.94      | 2.10       | 0.63       | $-0.11$    | 0.68       | $-0.62$    | 0.91       | $-2.99$    | 1.11      |
|                | $15^\circ$ | 6.69       | 1.36       | 4.75       | 1.29      | 3.50       | 1.26       | 0.75       | 0.89       | 0.10       | 0.95       | $-2.61$    | 1.18      |
|                | $25^\circ$ | 8.32       | 1.60       | 7.15       | 1.69      | 5.39       | 1.58       | 1.36       | 1.29       | $-0.08$    | 1.27       | $-3.70$    | 1.19      |

residual heading errors between the two experiments increased with the form FoE offset. A three-way (2 experiments × 6 form FoE offsets [$±5^\circ$, $±15^\circ$, and $±25^\circ$] × 6 headings) repeated measures ANOVA analysis in the residual heading error showed that the interaction between experiments and form FoE offsets was significant ($F(5,290) = 2.75, p = 0.019, \eta^2 = 0.045$). Newman-Keuls post hoc analysis showed that only when the form FoE offset was $25^\circ$, the residual heading error of Experiment 1b (Mean ± SE: 2.84 ± 0.65) was significantly larger than Experiment 1a (0.78 ± 0.65) ($p = 0.028$) (Figure 4e). The result suggests that the differences in heading error between the two experiments were not very evident, indicating that the postperceptual stages may not be involved in the effect of the previous form information on the heading estimation from optic flow.

To sum up, the results of current experiment found that the heading estimate from optic flow was biased toward the previously seen form FoE, showing an attractive effect of the previous form. The attractive effect of the previous form occurred at the perceptual stage and might not be involved in the postperceptual stage (e.g., working memory).

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**Experiment 2: Previous form effect occurs at the perceptual stage**

Experiment 1 found that the previous form information had an attractive effect on heading estimation from optic flow. Namely, heading estimates from the optic flow would be biased toward the previously seen form FoE. Additionally, Experiment 1 showed that the effect occurred at the perceptual stage instead of postperceptual stages. After checking Experiment 1, we found two factors that might lead us to fail to reveal the involvement of the postperceptual stages.

One was the sampling bias. We randomly enrolled two groups of participants to conduct the experiments. The results showed that the data variances of Experiments 1a and 1b were very different. Hence, the insignificant difference in heading errors between the two experiments could be due to the sampling bias. This proposal could be directly rejected. Because we initially enrolled 20 participants for Experiments 1a and 1b. The results also showed a weak interaction between experiments and form FoE offsets. At that time, we
suspected it was due to the sampling bias. Therefore we enrolled another 10 participants for each experiment. Unexpectedly, the results of the 10 participants were similar to those of the previous 20 participants. Hence, the sampling bias should not be the cause of the failure to reveal the involvement of the postperceptual stage.

The other was the experimental design. Specifically, in the form perceptual load condition of Experiment 1, the form stimulus was presented while participants were not asked to remember the position of the form FoE. During the experiment, some participants might keep some information of form in postperceptual stages (e.g., working memory). That is, the form information also took up some resources of postperceptual stages. As a result, the difference in the involvement of the postperceptual stage between the two experiments was shrunk, leading to insignificant differences between the two experiments.

To explore whether the effect of previous form on the heading estimation from optic flow occurred at the perceptual and postperceptual stages, participants conducted four blocks of trials. Each block corresponded to one condition: form-absent with integer-adding, form-presented with integer-adding, form-absent without integer-adding, and form-presented without integer-adding conditions. In the former two conditions, two integers were presented at the center of the first blank display (Figure 5a) or the form stimulus (Figure 5b). Participants were asked to sum the two integers. Each trial ended with one integer, and participants compared the integer and the sum. The integer comparison task could inhibit the postperceptual processing of the form information and thus increased the relative contribution of the perceptual processing. The procedure of form-absent and form-presented without integer-adding conditions were the same as the form-absent and form memory load conditions in Experiment 1 (Figures 3a and 3c). It was expected if the effect of the previous form occurred at the perceptual stage, then the differences in heading error would be significant between form-absent with integer-adding and form-presented with integer-adding conditions. Then, we used the form-absent with integer-adding condition to serve as the baseline of the form-presented with integer-adding condition and calculated the residual heading errors that were proposed to be originated from the perceptual stage. Similarly, we calculated the residual heading errors between the form-absent and form-presented without integer-adding conditions. The residual heading errors were proposed to be originated from the perceptual and postperceptual stages. If the effect of the previous form occurred at the perceptual stage, then the difference in the residual heading error would be significant between the with and without integer-adding conditions.

**Method**

**Participants**

Sixteen participants (seven males, nine females; 19–26 years old) were enrolled at Zhejiang Normal University. All were naïve to the experimental purposes.
and had normal or corrected-to-normal vision. The experiment was approved by the Scientific and Ethical Review Committee in the Department of Psychology of Zhejiang Normal University. The written consent form was obtained from each participant before they participated in the experiment.

Stimuli and apparatus
The stimuli and apparatus were similar to those in Experiment 1, except that the form FoE included ±20°. Additionally, the integers in the first blank display or form stimulus were randomly selected from the range [0, 10]. The distance between the two integers’ center was 2°. The integer at the end of trial was selected from the range [0, 20]. Each integer was blue (RGB: [0 0 200]) and 1.15° H × 1.72° V.

Procedure
The experimental procedure was similar to Experiment 1, except that each participant conducted four blocks of trials. Each block corresponded to one condition: form-absent with integer-adding, form-presented with integer-adding, form-absent without integer-adding, and form-presented without integer-adding conditions. Figure 5a illustrates the procedure of one trial in the form-absent with integer-adding condition. Each trial started with a 500-ms fixation point, followed by a 500-ms blank display with two integers. Participants were asked to add the integers and keep the sum in their minds. After a 200-ms blank display, an optic flow stimulus was presented for 500 ms. Then, a white horizontal line with a blue mouse-controlled probe was on the display center. Participants were asked to indicate the heading estimate from optic flow by adjusting the probe position. After their response and a 200-ms blank display, a new integer was on the display center. Participants were asked to click the mouse button to report whether the new integer was larger than the sum. After they clicked the mouse button, the next trial started. The trial procedure of the form-presented with integer-adding condition was the same as that of the form-absent with integer-adding, except two integers were presented at the center of one form stimulus (Figure 5b). The trial procedures of the form-absent and form-presented without integer-adding conditions were the same as the form-absent condition (Figure 3a) and the form memory load condition in Experiment 1 (Figure 3c).

Form-absent with and without integer-adding conditions consisted of 96 trials each (16 trials × 6 headings). Form-presented with and without integer-adding conditions consisted of 192 trials each (16 trials × 2 form FoE offsets × 6 headings).

Experiment contained a total of 576 trials. The experiment lasted for about 1.5 hours.

Data analysis
A two-way (3 form FoE offsets [form-absent, ±20°] × 6 headings) repeated-measures ANOVA analysis was adopted to examine whether the heading errors were significantly different between form-absent and form-presented with integers conditions. If the main effect of form FoE offsets was significant, then the previous form information affected the heading estimation from optic flow, and the effect of the previous form occurred at the perceptual stage. The same analysis procedure was applied to form-absent and form-presented without integers conditions.

Next, we calculated the residual heading error, which was the difference in heading error between the conditions of form-present and form-absent with integer-adding, or without integer-adding, respectively. A three-way (2 integer-adding [with vs. without] × 2 form FoE offsets [±20°] × 6 headings) repeated measures ANOVA analysis was adopted to examine whether the residual heading error was significantly different between the two integer-adding conditions. If the main effect of integer-adding was significant or the interaction between integer-adding and form FoE offsets was significant, and the Newman-Keuls post hoc analysis showed that effects of integer-adding varied with form FoE offsets, then the effect of the previous form occurred at postperceptual stages.

Result and discussion
We first examined whether participants followed instructions to finish the integer-adding task and form FoE reproduction task. For one thing, one-sample t-testing showed that the accuracies of integer-adding tasks was significantly larger than 0.5 in the form-absent with integer-adding condition (Mean ± standard deviation: 0.92 ± 0.92, t(16) = 7.16, p < 0.001, Cohen’s d = 2.53) and the form-presented with integer-adding condition (0.91 ± 0.92, t(16) = 7.21, p < 0.001, Cohen’s d = 2.55), suggesting that participants well finished integer-adding task following the instructions.

Figure 6d plots the perceived form FoE against the actual form FoE. It shows that although the accuracy was low, the perceived FoE increased with the actual FoE, suggesting that participants followed the instruction to remember the form FoE.

Figures 6a and 6b plot the heading error against the actual heading. “Left” and “Right” on the x-axis mean the actual heading to the left or right of the display center (0 degrees). “Left” and “Right” on the
Figure 6. Results of Experiment 2. (a) and (b) The heading error against the actual heading for the conditions with and without integer-adding. “Left” and “Right” on the x-axis mean the actual heading is left or right to the display center (0°). “Left” and “Right” on the y-axis mean the heading estimate to the left or right of the actual heading. The blue and red markers indicate that the conditions with and without integer-adding, where the circle and dot markers represent the form FoE to the left or right of the flow FoE. Blank markers indicate the form-absent condition. Each marker represents the mean heading error averaged across 16 participants. The error bar represents the standard error across 16 participants. (c) The residual heading error against the actual heading. “Left” and “Right” on the y-axis indicate that the heading error of the form-presented condition is left or right to that of the form-absent condition. Each marker represents the mean residual heading error averaged across 16 participants. The error bar represents the standard error across 16 participants. (d) Results of the form FoE reproduction task in Experiment 2. “Left” and “Right” on the x-axis (y-axis) mean that the actual (perceived) form FoE is left or right to the display center (0°). Each dot represents the mean perceived form FoE averaged across 16 participants. The error bar represents the standard error averaged across 16 participants.

y-axis mean the heading estimate is left or right to the actual heading. “Left” and “Right” on the legend mean that the form FoE is left or right to the heading from optic flow. The figures show that compared with the form-absent condition (black dots), when the form FoE is left to the heading from optic flow (blue or red circles), the heading error is more left-biased; on the contrary, when the form FoE is right to the heading from optic flow (blue or red dots), the heading error is more right-biased. This suggests that the heading
estimation from optic flow was biased toward the previous form FoE, showing an attractive effect of the previous form.

One two-way (3 form FoE offsets × 6 headings) repeated-measures ANOVA analysis showed that in the conditions with integer-adding, the main effect of form FoE offsets was significant ($F(2, 30) = 5.35, p = 0.010, \eta^2 = 0.26$). Newman-Keuls post hoc analysis showed that in the condition of with integer-adding, the heading error of the −20° form FoE offset (Mean ± SE: −1.98 ± 0.58) was significantly left-biased than the heading errors of the form-absent condition (−0.31 ± 0.65) and the 20° form FoE offset (0.052 ± 0.73) ($p < 0.012$); the heading errors were not significant between the latter two condition ($p = 0.59$). The interactions between form FoE offsets and headings were not significant ($F(10, 150) = 0.96, p = 0.48, \eta^2 = 0.060$). These results suggest that the heading estimates from optic flow are biased toward the previous form FoE, showing an attractive effect of previous form, which occurs at the perceptual stage.

The result pattern of the condition without integer-adding was similar to that of the condition with integer-adding, the main effect of form FoE offsets was significant ($F(2, 30) = 3.72, p = 0.036, \eta^2 = 0.20$). Newman-Keuls post hoc analysis showed that the heading error of the form-absent condition (−2.38 ± 0.85) was significantly left-biased than the heading error of the 20° form FoE offset condition (1.06 ± 1.30) ($p = 0.29$); the heading error of the form-absent condition (−1.00 ± 0.71) was between the heading errors of ±20° form FoE offsets but was not significantly different from the heading errors of ±20° form FoE offsets ($p > 0.11$). The interaction between form FoE offsets and headings was not significant in the conditions of without integer-adding ($F(10, 150) = 0.87, p = 0.56, \eta^2 = 0.055$). These results suggest an attractive effect of the previous form in heading estimation from optic flow.

To examine whether the attractive effect of the previous form occurred at postperceptual stages, we calculated the residual heading errors of the conditions without and with integer-adding. One three-way (2 integer-adding [with vs. without] × 2 form FoE offsets [±20°] × 6 headings) repeated measures ANOVA analysis showed that the main effect of integer-adding was not significant ($F(1,15) = 1.29, p = 0.27, \eta^2 = 0.079$). None of the interaction effects between the integer-adding and other factors were significant ($p > 0.46$), suggesting that the attractive form effect did not occur at the postperceptual stages. Additionally, the residual heading error of −20° form FoE offset (−1.57 ± 0.52) was more left-biased than that of 20° form FoE offset (1.15 ± 0.60) ($F(1,15) = 10.58, p = 0.0054, \eta^2 = 0.41$), suggesting an attractive effect of the previous form in heading estimation from optic flow.

To sum up, Experiment 2 showed that humans would bias their heading estimate from optic flow toward the previous form FoE, showing an attractive effect of the previous form. Importantly, the form effect occurred at the perceptual stage, not postperceptual stages (e.g., working memory). These findings were consistent with Experiment 1.

### General discussion

Combining the results of two experiments, we found that the current heading estimation from optic flow was biased toward the previously seen form FoE, showing an attractive effect of previous form information, and the effect occurred at the perceptual stage. Our findings suggest that observers can combine optic flow and form information across the temporal domain to estimate heading.

### Integration of form and optic flow

Our finding that static form and dynamic optic flow can be integrated across the temporal domain provides further evidence for the claim that the processing of form and motion is closely linked rather than independent. It has been debated whether the processing of static form and dynamic motion information is distinct or closely linked. Researchers initially proposed that motion and form are processed by two distinct pathways originating in the primary visual cortex (V1). The dorsal visual cortices (known as the “where” pathway) process motion information, whereas the ventral visual cortices (known as the “what” pathway) process form information (DeYoe & Van Essen, 1988; Mishkin, Ungerleider, & Macko, 1983). This proposal has been supported by a wealth of evidence from brain-damage patients (Benson & Greenberg, 1969; Goodale & Milner, 1992; Zihl, von Cramon, & Mai, 1983). However, many recent studies have suggested that the processing of motion and form information can be closely linked (Kourtzi, Krekelberg, & van Wezel, 2008). For instance, Or, Khuu, and Hayes (2010) found that the estimates of global form orientation were affected by the concurrently presented global motion direction and vice versa; Edwards and Crane (2007) found that the form information (i.e., motion streaks) could improve the detection sensitivity of global motion patterns. Note that the motion stimuli used in these studies are simple two-dimensional dot patterns that are mainly processed in V1 (Geisler, 1999; Tang, Dickinson, Visser, & Badcock, 2005). In contrast, the motion stimulus generated by observers’ self-motion (i.e., optic flow) are more complex and processed by high visual cortices (e.g., MST, Duffy & Wurtz, 1997;
Cardin, Hemsworth, & Smith, 2012). Niehorster et al. (2010) first demonstrated that observers could optimally integrate concurrently presented form and optic flow to estimate their heading (also see Kuai et al. 2020), suggesting that the integration of motion and form is applied to simple and complex stimuli. On this basis, our finding indicates that the integration also occurs across the temporal domain and enriches previous studies.

Tang et al. (2005) explored the effects of previous Gabor orientation on the estimation of motion direction and found the current estimate of motion direction was biased toward the previous orientation, showing an attractive effect. This finding was consistent with our study. However, Tang and his collaborators adopted an aftereffect paradigm in which the Gabor stimulus (adapter) was presented for 3 seconds, resulting in an orientation aftereffect superimposed on the motion stimuli. From this perspective, the form and motion can be regarded as concurrently presented. In contrast, our 500-ms short form stimulus would not generate an aftereffect that could ensure the dissociation of form and optic flow.

**Perceptual stage in the effect of previous form**

Another interesting finding was that the effect of the previous form on heading estimation from optic flow occurred at the perceptual stage. The occurrence mechanisms (perceptual vs. postperceptual) of the information have been debated a lot. However, there was not a consistent conclusion. According to some studies, integrating previous and current information mainly occurs at the perceptual stage (Cicchini et al., 2017; Fischer & Whitney, 2014; Manassi et al., 2018). Some also pointed out the serial dependence could lead to a perceptual illusion that was independent of postperceptual stages (e.g., memory, Manassi, Mauro, & Whitney, 2022) or occurred through serial dependence in low-level templates (Murai & Whitney, 2021b). These all suggest that serial dependence is a manifestation in perception. In contrast, others highlighted the role of the postperceptual stage in serial dependence (Ceylan et al., 2021; Bliss, Sun, & D’Esposito, 2017; Fritsche et al., 2017; Pascucci et al., 2019). Additionally, there are some studies uncovering that both stages were involved in the integration (e.g., Bae & Luck, 2020; Fornaciai & Park, 2020). Our current findings provide further evidence for the claim that the serial dependence is a manifestation in perception.

**Future research directions**

Previous work on the integration of multimodal information mainly focuses on two aspects. One is the occurrence mechanisms of the integration. That is, does the integration occur at the perceptual stage or postperceptual stages? Our current study answered the occurrence mechanisms of the integration of current optic flow and previous form and revealed that the integration occurred at the perceptual stage.

The other aspect is the computational mechanisms of the integration of multi-model information. That is, do neural systems optimally integrate different information following Bayesian inference theory (Bernardo & Smith, 1994; Cox, 1946; Jaynes, 1986)? For example, Niehorster et al. (2010) varied the coherence level of dot pairs that constituted form stimuli and found that as the reliability of flow information decreased, observers would rely more on optic flow to estimate their heading (Figure 1c), which an ideal observer model well predicted (Sun et al., 2020; Xing & Saunders, 2016). Cicchini et al. (2017) varied the spatial frequency of Gabor patches to manipulate the reliability of orientation stimuli. Their results showed that as the reliability of stimuli decreased, observers would rely more on the previous stimulus to estimate the current orientation, which was also consistent with an ideal observer model. Fritsche, Spaak, and de Lange (2020) found that integrating current and previous homogenous information followed efficient coding and Bayesian decoding theories (Wei & Stocker, 2015). Therefore future studies can explore the computational mechanisms of integrating the previous form and current optic flow.

Additionally, our current study explored how the previous form information and the current optic flow integrated with psychophysical methods. Next, we can consider using neuro-electrophysiological or brain-imaging techniques (e.g., EEG, TMS, fMRI) to uncover the neural basis of the integration of two types of information. For instance, the fMRI study of Kuai et al. (2020) found that area V3B/ KO was in charge for integrating the simultaneously appeared form and optic flow to estimate heading. John-Saaltink, Kok, Lau, and De Lange (2016) found cortical area V1 can be responsible for the integrating the previous and current orientation information. Using EEG and MVPA techniques, Bae and Luck (2020) found that integrating of previous and current orientations occurred at the perceptual and postperceptual stages. In conclusion, these neurophysiological studies have provided a solid platform for us to explore the neural basis of integrating previous form and current optic flow.

In summary, investigating the occurrence, computational and neural mechanisms underlying the integration of the previous form and current optic flow will enable us to comprehensively comprehend the integration of multimodal information across the temporal domain.

**Keywords:** heading perception, optic flow, form information, perceptual stage, history effect
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Footnote

1Here, we found a weak interaction effect with the repeated measures ANOVA analysis, and the post hoc analysis only revealed one significant difference pair. Hence, we did another type of analysis. Specifically, we fitted the residual heading error as a function of the form FoE offset for the two experiments. Appendix Figure A1 shows the results. Independence sample t-test show that the differences in the slope were not significantly different between two experiments (t(32.35) = −1.68, p = 0.10, Cohens' d = 0.44), suggesting that the effect of previous form information on heading estimation from optic flow might not occur at the postperceptual stage.

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### Appendix

A two-way (7 form FoE offsets × 6 headings) repeated measures ANOVA analysis showed that the main effect of form FoE offsets was significant $F(6, 174) = 7.97, p < 0.001, \eta^2 = 0.22)$. Newman-Keuls post hoc analysis showed that the heading errors of the 15-degree, 25-degree form FoE offsets (Mean ± SE: $−2.20 ± 0.78, 3.07 ± 1.09$) were more right biased than the form-absent condition ($−0.23 ± 0.48$) ($p = 0.041, p = 0.0026$); and the heading error of $−25°$ form FoE offset ($−1.43 ± 0.78$) was more left biased than the $5°, 15°, 25°$ form FoE offsets ($p = 0.015, p < 0.001, p < 0.001$). These results suggested that the heading estimate from optic flow would be biased toward the previous form FoE.

The interaction between form FoE offsets and headings was significant ($F(30,870) = 1.62, p = 0.020, \eta^2 = 0.053$). Newman-Keuls post hoc analysis showed that when the heading was $18°$ and $30°$ (right to the display center), and the previous form FoE was right to the actual heading (i.e., form FoE offsets: $5°, 15°$), the sizes of the left bias of the heading error were significantly reduced, compared with the heading errors in the form-absent condition (see “Right” red-system and grey bars in Figure 4c), which meant the heading estimate was attracted to the previous right-side form FoE; similarly, when the heading was $−30°$ (left to the display center), and the previous form FoE was left to the actual heading (i.e., form FoE offsets: $−5°, −15°, −25°$), the sizes of the right bias of the heading error were also significantly reduced, compared with the heading errors in the form-absent condition (see “Left” red-system and grey bars in Figure 4c), which meant the heading estimate was attracted to the previous left-side form FoE.