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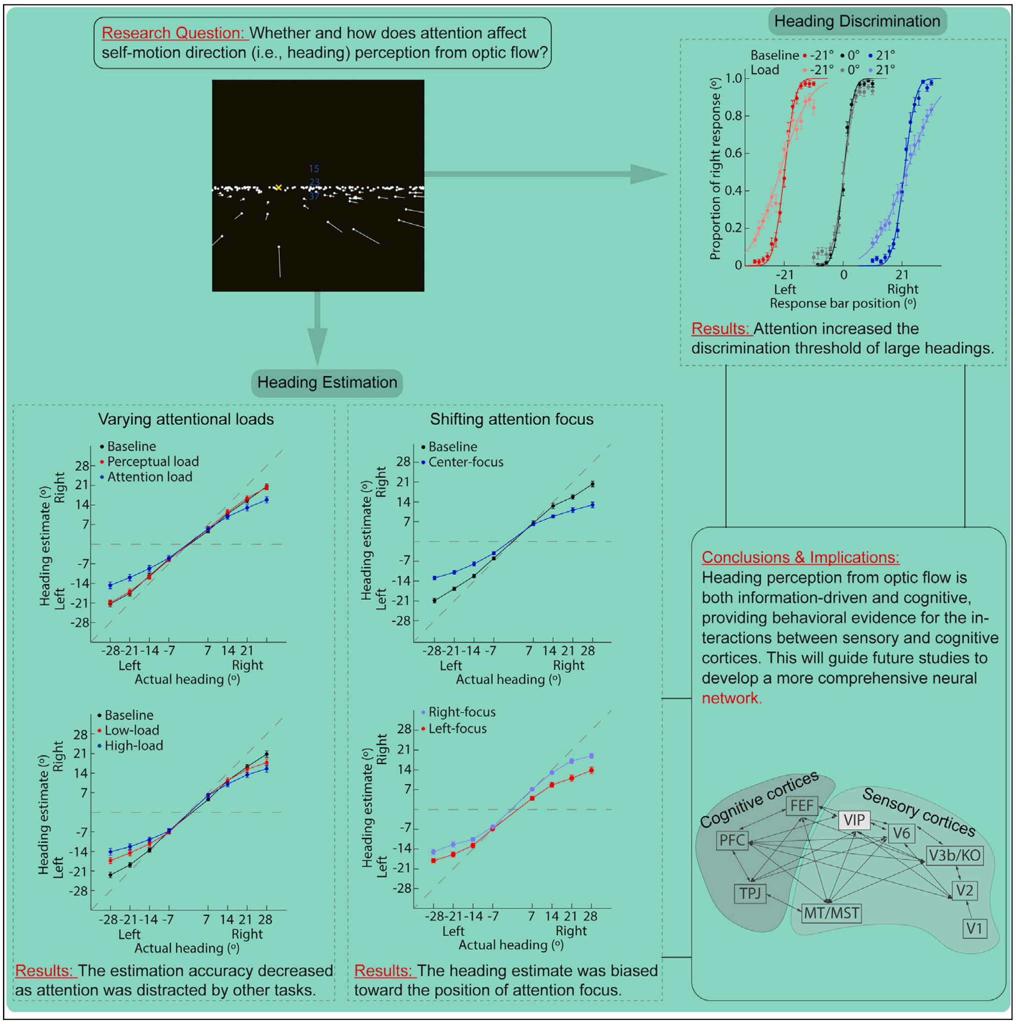

Qi Sun, Lin-Zhe Zhan, Fan-Huan You, Xiao-Fei Dong

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Highlights

The results show that attention affects the peripheral headings from optic flow

Showing that heading perception from optic flow is sensory and cognitive

The findings are against the previous pure information-driven claim

Providing evidence for the interaction between cognitive and sensory cortices

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Attention affects the perception of self-motion direction from optic flow

Qi Sun,[1,2,3,4,*] Lin-Zhe Zhan,[1] Fan-Huan You,[1] and Xiao-Fei Dong[1]

SUMMARY

Many studies have demonstrated that attention affects the perception of many visual features. However, previous studies show conflicting results regarding the effect of attention on the perception of self-motion direction (i.e., heading) from optic flow. To address this question, we conducted three behavioral experiments and found that estimation accuracies of large headings (>14°) decreased with attention load, discrimination thresholds of these headings increased with attention load, and heading estimates were systematically compressed toward the focus of attention. Therefore, the current study demonstrated that attention affected heading perception from optic flow, showing that the perception is both information-driven and cognitive.

INTRODUCTION

Accurately perceiving the self-motion direction (i.e., heading) is a fundamental function of our visual system and is essential for our survival. Many studies have demonstrated that optic flow—the dynamic motion pattern projected on the retina when observers move in the world[1]—is a crucial piece of retinal information used to efficiently perceive heading directions.[2,3] When moving along a straight line, observers can accurately estimate their heading direction by localizing the position of the focus of expansion (FoE) in optic flow (yellow crosses in Figure 1A).[4–12]

Several studies have proposed that heading estimation from optic flow is mainly information-driven. Attention, a cognitive ability, is barely involved.[5,11] For instance, Royden and Hildreth (1999)[5] showed participants a series of stimuli containing a moving object and an optic flow. In some trials, participants paid attention to the optic flow while ignoring the object; in other trials, participants paid attention to the object while ignoring the optic flow. They found that heading estimation errors were not significantly different between the two conditions. In contrast, the accuracy of object motion direction was higher when attention was more allocated to the object than when that was more allocated to the optic flow. They, therefore, concluded that heading perception from optic flow did not require much attention.

Duffy and Wurtz (1991a, 1991b)[13,14] were the first to discover that neurons in the dorsal medial superior temporal cortex (MSTd) selectively respond to the FoE in optic flow. It has been demonstrated that MSTd is involved in estimating heading directions from optic flow.[15,16] Dubin and Duffy (2007, 2009)[17,18] found that when attention was distracted by other stimuli, some neurons in MSTd had reduced sensitivity, as evidenced by a decrease (increase) in the peak (width) of their tuning curves. Additionally, the activities of certain neurons decreased as the distance between the attention focus and the FoE increased. These findings suggest that estimating headings from optic flow requires attention, which contradicts Royden and Hildreth (1999).[5]

After comparing these studies, it was found that the heading directions in Royden and Hildreth (1999)[5] were selected from 4°, 6°, 8°, and 10° relative to the display center, whereas the heading directions in Dubin and Duffy (2007, 2009)[17,18] were 30° away from the display center. Given these facts, it is proposed that conflicting results regarding the effect of attention on the heading estimation from optic flow could be due to the heading range. In other words, attention could significantly affect the estimation of large headings (i.e., >10°). This was examined in the current study.

In summary, the current study conducted three behavioral experiments to systematically examine whether and how attention affected heading perception from optic flow. In Experiment 1, participants were asked to estimate heading directions from optic flow. In some trials, participants were also asked to conduct a number-addition task with different difficulties, generating different levels of attention loads. We found that the accuracy of heading estimation decreased with increasing attention load, suggesting that attention affected heading estimation from optic flow. Experiment 2 shifted the position of the focus of attention and found that heading estimates were compressed toward the focus of attention. Experiment 3 examined the effects of attention on heading discrimination sensitivity and found that the discrimination sensitivity decreased with the increase in the attention load.

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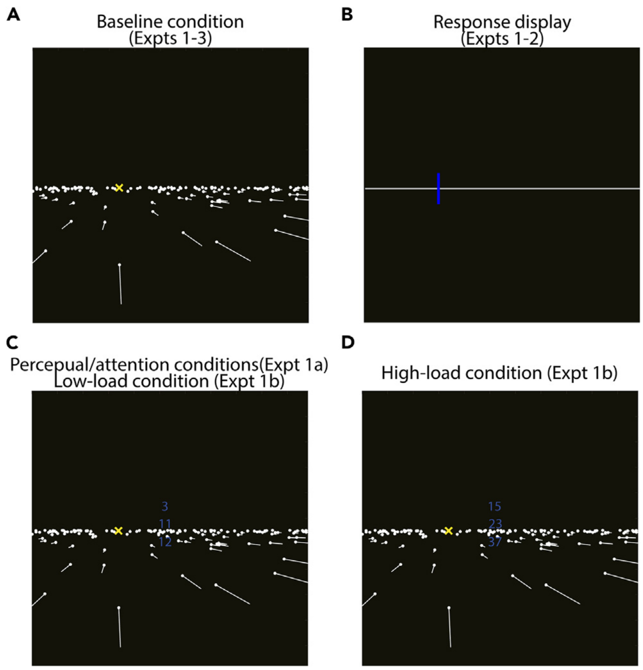

Figure 1. Stimulus displays used in the current study

(A) White dots indicate the positions of dots in the 1st frame of the stimulus. White lines indicate the motion trajectories of dots in the following frames. The yellow cross indicates the simulated heading direction. The white lines and yellow crosses are invisible in the experiment.

(B) Response display for heading estimation that contains a horizontal line and a vertical blue probe controlled by mouse. Participants were asked to change the position of the probe to indicate their perceived heading.

(C) and (D) Three integers are presented vertically in the center of the optic flow display.

Uncovering the effects of attention on heading perception from optic flow suggests that heading perception from optic flow is both information-driven and cognitive, enriching the previous studies.[7,12,19] This finding helps researchers comprehensively understand the cognitive process underlying heading perception from optic flow and opens several avenues for future studies.

RESULTS

Attention affects heading estimation from optic flow

We first examined whether attention load affected the heading estimation from optic flow that simulated observers moving on a dot-ground (Figure 1A) (Experiment 1a) and how the estimation accuracy was changed with increasing the attentional load (Experiment 1b). To address the aforementioned questions, we asked participants to report their perceived heading directions by moving a mouse-controlled probe on a horizontal line (Figure 1B).

Experiment 1a included three conditions: in the baseline condition, only optic flow was presented (Figure 1A); in the perceptual condition, three integers were positioned vertically in the center of optic flow (Figure 1B) and participants were asked to estimate headings but ignore the integers; in the attention condition, the stimulus was similar to the perceptual condition, but participants were asked to finish a number-addition task before estimating the heading direction. In the number-addition task, participants compared the sum of the first two integers with the third integer (Please read the procedures in STAR Methods for details.)

Figure 2A plots results of Experiment 1a. The oblique dashed line indicates the perfect performance, meaning that the perceived heading is equal to the actual heading; the horizontal dashed line indicates the purely center bias, meaning that the perceived heading is always 0°, regardless of the actual heading. The accuracy of heading estimation decreased with the increase in the bias of heading estimates away from the oblique dashed line. It clearly shows that the heading estimates of the attention condition (blue lines and dots) were more biased toward the display center than the baseline (black lines and dots) and perceptual (red lines and dots) conditions. The heading estimates of the latter two conditions are overlapped. One 3 (experimental conditions) × 8 (headings) repeated measures ANOVA analysis on heading estimates showed that the interaction between the two factors was significant ($F(14, 238) = 20.12$, $p < 0.001$, $\eta^2 = 0.54$). Newman-Keuls post-hoc analysis showed that across all headings, there was no significant difference in the heading estimate between baseline and perceptual conditions ($ps > 0.33$); whereas the heading estimates of attention condition were smaller than that of baseline and perceptual conditions ($ps < 0.0056$) except that when the actual heading was $\pm 7°$ and 14° ($ps > 0.076$). The results suggested that attention affected heading estimation from optic flow, especially for the large headings (e.g., >14°).

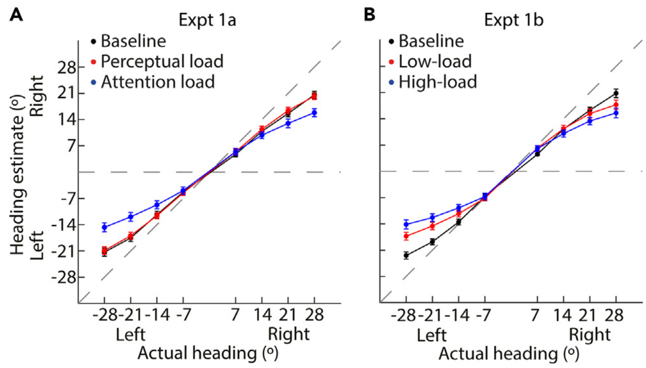

Figure 2. Results of Experiment 1

(A) and (B) Heading estimate is against actual heading in Experiments 1a and 1b. Left (right) on the x axis or y axis means that the actual heading or the heading estimate is left (right) to the display center (0°). Dots represented the mean heading estimate averaged across all participants. Error bars were standard errors across all participants.

Based on Experiment 1a, Experiment 1b varied the difficulties of number addition tasks to create the low- and high-load conditions (Figures 1A, 1C, and 1D). Figure 2B clearly that when the attention load increased, the estimation accuracy decreased further. One 3 (experimental conditions) × 8 (headings) repeated-measures ANOVA showed that the interaction between the two factors was significant ($F(14, 224) = 12.10$, $p < 0.001$, $\eta^2 = 0.43$). Newman-Keuls post-hoc analysis showed that when the actual headings were $\pm28°$, $\pm21°$, and $-14°$, the heading estimates in the high load condition tended to be significantly smaller than that in the low load condition (*ps* < 0.083), the latter was also significantly smaller than that in the baseline condition (*ps* < 0.016). There was no significant difference between the other conditions (*ps* > 0.10). Together, Experiment 1b showed that the estimation accuracy of large headings (e.g., >14°) decreased with increasing attention load.

Heading estimates are biased toward the focus of attention

Dubin and Duffy (2007, 2009)[17,18] found the tuning functions of MSTd neurons were modulated by the relative distance between the attention focus and the heading direction. In Experiment 1, we fixed observers' attention focus on the display center and found that attention mainly affected the estimation of large headings (e.g., >14°). In Experiment 2, we directly manipulated the position of attention focus with a rapid serial visual presentation (RSVP, Figure 3) paradigm to examine whether and how the position of attention focuses affected heading estimation from optic flow. It should be noted that aside from estimating heading directions, participants were asked to press space key as quickly as possible when they saw a number (please read procedures in STAR Methods for details). Additionally, we examined whether the effects of attention on heading estimation could be reproduced in different experimental designs (e.g., RSVP).

In Experiment 2a, participants were asked to finish two blocks of trials, each corresponding to one condition (center-focus vs. baseline). In the center-focus condition (Figure 3B), five character displays were sequentially presented on the display center. An optic flow display was presented after the 2nd, 3rd, or 4th character display, followed by participants' heading responses (Figure 1B). In the baseline condition, the character displays were placed with blank displays (Figure 3A). In Experiment 2b, the characters were replaced on the left side of the display center by 10°, guiding the attention focus to the left side (left-focus condition, middle panel in Figure 3C).

More than 89.71% of numbers were captured by participants (Experiment 2a: Mean ± SD, 0.91 ± 0.031; Experiment 2b: 0.90 ± 0.020), suggesting participants well finished the RSVP task. Figures 4A and 4B plot the results of heading estimation in Experiments 2a and 2b. They show that when attention is distracted by the character displays (center- and left-focus conditions), the accuracies of the heading estimation are reduced, consistent with Experiment 1.

To examine whether attention focus affected heading estimation, we calculated the normalized estimation difference (NED) in each heading, given by:

$$NED = \frac{HE_{focus} - HE_{baseline}}{HE_{baseline}} \quad \text{Equation 1}$$

In which, HE_{focus} was the heading estimate of the center-focus condition (Experiment 2a) or the left-focus condition (Experiment 2b). $HE_{baseline}$ was the heading estimate of the baseline condition (Experiments 2a or 2b). Figure 4C plots the NED results. One 2 (focus positions) × 8 (headings) mixed-repeated measures ANOVA showed that the interaction between two factors was significant ($F(7, 210) = 5.19$, $p < 0.001$, $\eta^2 = 0.15$). Further post-hoc analysis showed that when actual headings were $-28°$, $-21°$, $-14°$, the NEDs of the left-focus condition were significantly smaller than that of the center-focus condition (*ps* < 0.045), and when the actual heading was 7° and 14°, the NEDs of the left-focus condition were tend to be larger than that of the center-focus condition (p < 0.064). These results suggested that the heading estimates were systematically compressed toward the focus of attention.

In Experiments 2a and 2b, we asked participants to fixate on the display center, but it could not guarantee that participants did not move their eyes. To test whether eye movements played a role in this process, we asked participants to finish two blocks of trials in Experiment 2c,

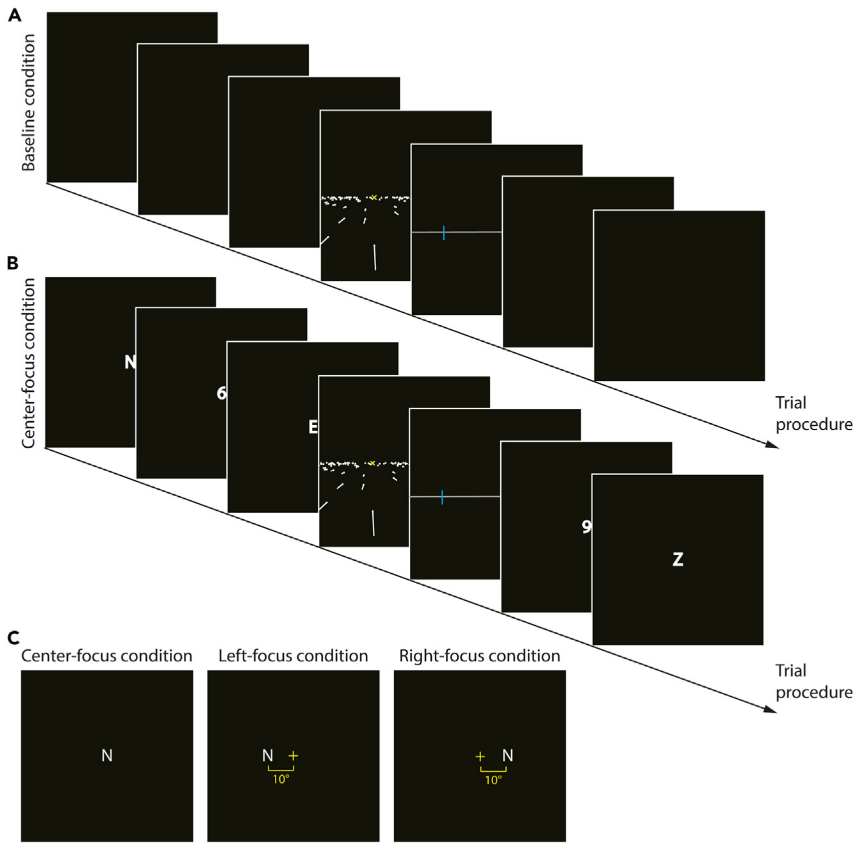

Figure 3. Trial procedure of RSVP paradigm used in Experiment 2

(A) Baseline condition. Five blank displays are sequentially presented. Each last for 150 ms, followed by a 50-ms gap. Participants were asked to press SPACE key as quickly as possible when seeing a number. An optic flow display (200 ms) and response display (disappeared until response) are presented after the 2nd, 3rd, or 4th blank display. The illustration shows the case whether the optic flow was presented after the 3rd blank display.

(B) Center-focus condition. Five blank displays were replaced with five character displays. A letter or number was presented on the display center. Aside from reporting the heading direction, participants were asked to press "SPACE" key when they saw a number as quickly as possible.

(C) Three types of character displays: center-focus display in which the character was on the display center; left- or right-focus display in which the character was left or right to the display center by 10°. The yellow "+" indicates the display center. All yellow markers were invisible in the experiment.

each corresponding to the left- and right-focus condition (middle and right panels in Figure 3C). Importantly, participants' eye movements were recorded. If participants moved their eyes toward the focus of attention in the experiment, then the attention was overt attention, and vice versa. Like Experiments 2a and 2b, participants well finished the RSVP task in which more than 83.62% of numbers were captured by participants (Mean $\pm$ SD: 0.84 $\pm$ 0.015).

Figure 4C clearly shows that for the left-side headings, the estimation accuracies in the left-focus condition (red dots) were higher than those in the right-focus condition (light blue dots); the trend was reversed for the right-side headings. The results further confirmed the effects of attention on heading estimation.

Importantly, the horizontal and vertical positions of fixations were not affected by the focus conditions ($F(1, 11) = 1.18$, $p = 0.30$, $\eta^2 = 0.097$) (Figures 5A–5C), suggesting that participants well controlled their eyes in the left- and right-focus conditions, indicating that the attention was covert. Additionally, the main effect of headings on the horizontal position of fixations was significant ($F(7, 77) = 13.00$, $p < 0.001$, $\eta^2 = 0.54$). The fixations were more right-biased when the heading was right to the display center than when the heading was left to the display center. However, the largest bias induced by eye movements was about 2.58° when heading was 28°, much smaller than the 11.64° estimation error. Therefore, eye movements contributed little to the overall estimation error.

Discrimination threshold increases with the attention load

Experiments 1 and 2 examined the effects of attention on the heading estimate. In Experiment 3, aside from asking participants to estimate heading directions (0° and $\pm$21°), we also evaluated the thresholds of heading discrimination in different attention conditions. On each trial of the discrimination task in the baseline condition, an optic flow display was presented, followed by a vertical bar that was to the left or right of the heading direction by 0°, 1.5°, 3°, 4.5°, 6°, 7.5°, 9°, or 10.5°. Participants were asked to judge whether the heading direction was right or left

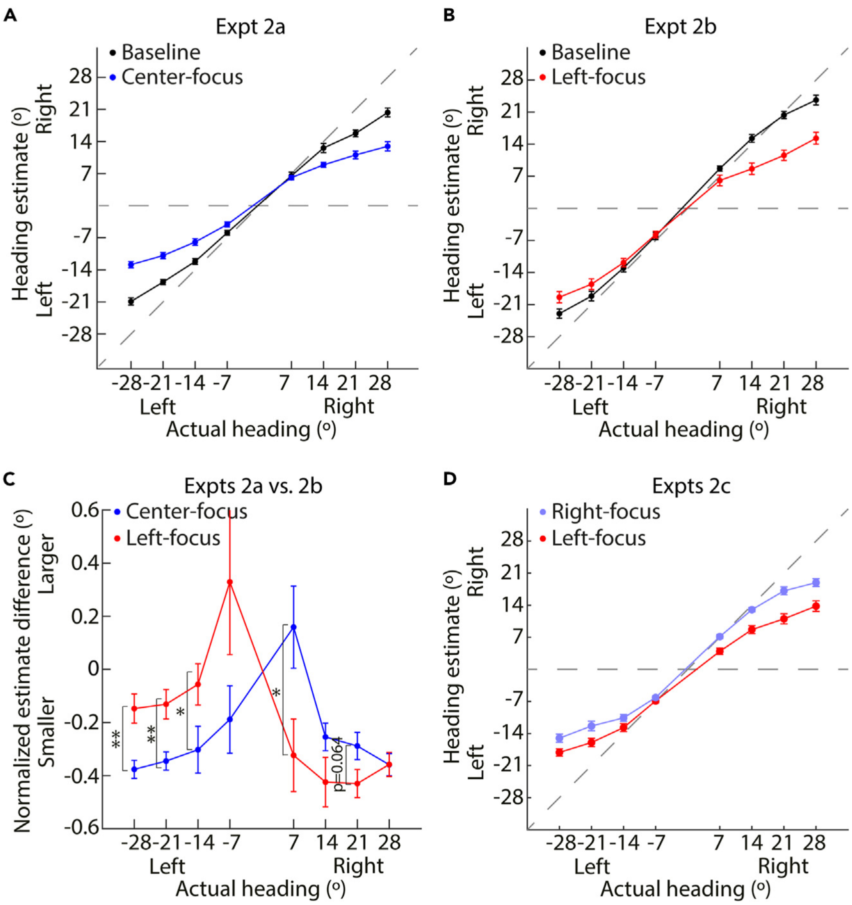

Figure 4. Results of Experiments 2

(A), (B), and (D) Heading estimate is against actual heading. Left (right) on the x axis or y axis means that the actual heading or the heading estimate is left (right) to the display center (0°). Dots represented the mean heading bias averaged across all participants. Error bars were standard errors across all participants.

(C) Normalized estimate difference (NED) is against actual heading. Smaller (larger) on the y axis means the heading estimate in the focus condition was smaller (larger) than that in the baseline condition. Blue and red markers correspond to the center- and left-focus conditions. Dots represented the mean NED averaged across all participants. Error bars were standard errors across all participants.*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

of the vertical bar. The trial procedure in the attention load condition was similar to that in the baseline condition, except that three integers were presented vertically (Figure 1C) and participants finished the number-addition task before discriminating headings (please read procedures in STAR Methods for details).

Figure 6A clearly shows that the estimation accuracy is lower in the load condition (red dots) than in the baseline condition (black dots), consistent with the baseline and high-load conditions in Experiment 1b (red and black diamonds).

To evaluate the discrimination threshold, we fitted the proportion of right-responses (PRR) in the discrimination task as a cumulation Gaussian function of the bar position (BP, the sum between the bar deviation and the actual heading) for each actual heading, given by:

$$PRR = 1 \Big/ 2 \times \left(\frac{1+\text{erf}(BP - \mu)}{\sqrt{2}\sigma} \right) \qquad \text{Equation 2}$$

In which, μ corresponds to the point of subjective equality (PSE); σ indicates the standard deviation of the cumulative Gaussian curve, which is proportional to the discrimination threshold. Large σ indicates higher discrimination threshold, indicating a lower precision of the internal representation.

Solid lines in Figure 6B show the best cumulative Gaussian curves. The steeper the curve, the smaller the standard deviation. Figure 6C plots the standard deviation against different conditions. A repeated measures ANOVA showed that the standard deviations of $\pm 21°$ in the baseline condition were significantly smaller than those in the load condition ($F(1, 14) = 40.17$, $p < 0.001$, $\eta^2 = 0.74$). The results suggested that attention load increased the discrimination thresholds of large headings (e.g., $\pm 21°$) but had little effect on small headings (e.g., 0°).

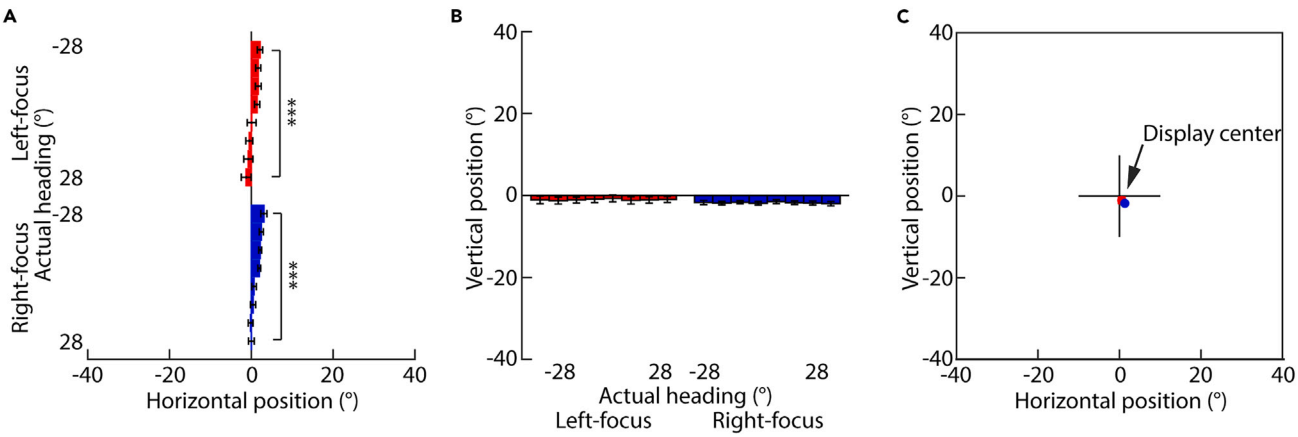

Figure 5. Eye-movement results of Experiments 2c

(A) and (B) Horizontal and vertical positions of fixations are against different headings and left- and right-focus conditions. Error bars were the standard errors.
(C) Average fixation positions in left- and right-focus conditions are plotted on a canvas of stimulus display. ***, $p < 0.001$.

DISCUSSION

The current study systematically investigated whether and how attention affected heading estimation from optic flow by conducting three behavioral experiments. The results showed that attention affected heading estimation accuracy and discrimination sensitivity, especially for the large headings (e.g., >14°). Both accuracy and sensitivity were decreased when attention was distracted by other tasks (e.g., the number addition task), consistent with the load theory of attention.[20–24] In addition, the heading estimate was biased toward the focus of attention. Therefore, the current study revealed that attention affects heading perception from optic flow, indicating that the heading perception is both information-driven and cognitive.

Implications of revealing effects of attention on heading perception

The current study systematically revealed that attention primarily affected the perception of large heading directions (e.g., >14°) from optic flow, resolving the controversial conclusions among previous studies.[5,17,18] Royden and Hildreth (1999)[5] found that attention barely affected heading perception from optic flow.[5] We extended their headings ([0°, 10°]) to the range of [-28, 28°] and found that attention mainly affected the large heading directions (e.g., 14°, 21°, and 28°). This expands the conclusion of Royden and Hildreth (1999).[5] Importantly, this finding is against the idea that heading perception from optic flow is mainly information-driven.[5,11]

Additionally, several recent studies have demonstrated that post-perceptual cognitive abilities, such as working memory, are involved in heading perception from optic flow.[7,12,19] The current study explicitly confirmed the involvement of attention, a cognitive ability that happens at both the perceptual and post-perceptual levels. This supports the idea that heading perception from optic flow is both information-driven and cognitive.

Prior research has revealed the effects of attention on "optic flow" processing.[5,17,18,25] However, the speeds of the dots in these "optic flow" patterns were increased from the FoE, as illustrated by the equation: $\cos(\alpha) \times \sin(\alpha)$, where α is the angle between the line of sight and each dot.[17,18] This type of motion patterns only simply captures the accelerating trend of the dots in optic flow. In contrast, the optic flow generated by self-motion is very complex (see Sun, 2020[26] for more details), which cannot be captured by the equation: $\cos(\alpha) \times \sin(\alpha)$. Therefore, although Dubbin and Duffy[17,18] called their stimuli "optic flow", they are actually non-optic flow. Sun Q. (2020)[26] evaluated the threshold of FoE discriminations of optic flow and non-optic flow patterns (e.g., the dots move at constant speeds or the positions of the dots were shuffled). They found that participants were more sensitive to discriminating expansion optic flow patterns than contraction optic flow patterns, whereas the trend was reversed for the non-optic flow patterns. This finding supports the processing difference between optic flow and non-optic flow. In addition, given that optic flow is highly ecological and experienced all the time, our visual system contains many cortical areas processing optic flow (see Sun , 2020[26] for a review). It can be boldly proposed that the processing of optic flow is mainly information driven and does not involve high-level cognitive abilities. Our findings contradict this proposal and extend the findings of Dubin and Duffy (2007, 2009)[17,18] to more real optic flow.

Furthermore, the optic flow in the current study simulated observers translating on the ground without moving eyes, head, and body, creating a radial flow pattern - one of the basic flow patterns (see Sun, 2020[26] for other types). Translation is the simplest self-motion in our daily lives. However, it is more common to move and rotate our eyes, head, and body simultaneously, resulting in a rotated flow.[3,26,27] Accurately perceiving heading from rotated flow is more difficult than from radial flow. Therefore, it is natural to rely on other information to improve heading estimation, such as the proprioceptive information provided by eye movements.[28–33] At the same time, moving eyes also changed the focus of (overt) attention. Wann et al. (2000)[34] found that heading perception from rotated flow was impaired when both covert and overt attention were distracted by a landmark, suggesting the effects of covert and overt attention on heading perception

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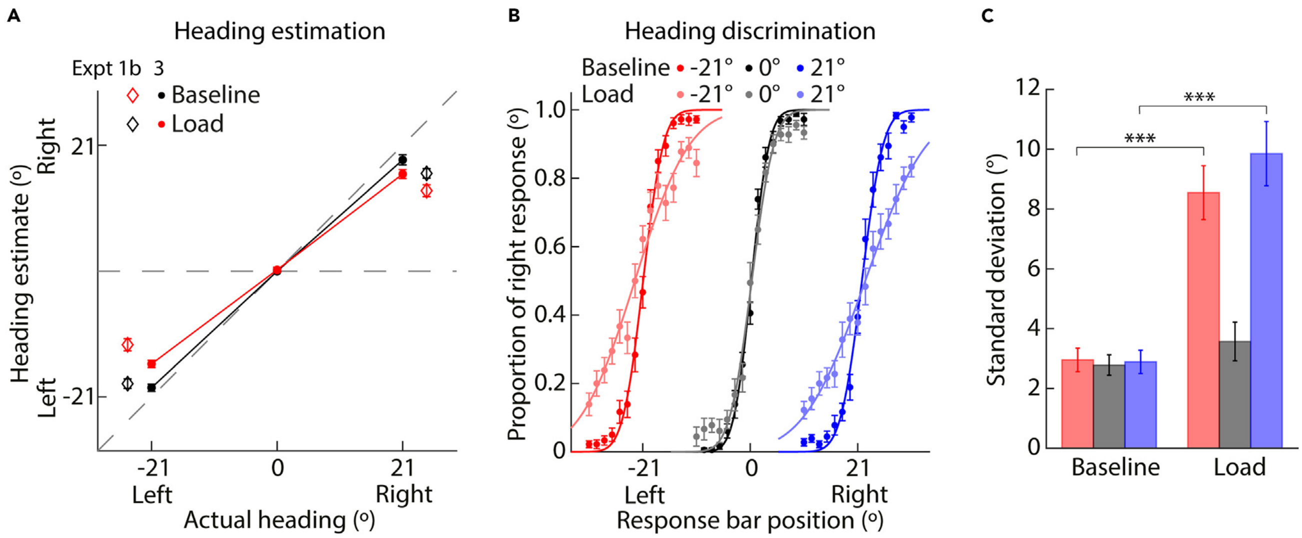

Figure 6. Results of Experiment 3

(A) Heading estimation results. Heading estimate is against actual heading. Left (right) on the x axis or y axis means that the actual heading or heading estimate is left (right) to the display center (0°). Error bars mean the standard error across all participants. The dot markers show the results of Experiment 3. Diamond markers show the results of Experiment 1b of the high-load conditions.

(B) Proportion of right responses (PRR) is against the response bar position. Error bars mean the standard error across all participants.

(C) Standard deviation is against the baseline and load conditions. Dots represented the mean heading bias averaged across all participants. Error bars are the standard deviations. ***, $p < 0.001$.

from rotated flow. On this basis, our current study extended their findings to simple optic flow and confirmed the role of covert attention in the processing of the simple optic flow.

Sun and Li (2019)[35] found that observers encoded their heading direction from optic flow using both allocentric (e.g., screen center) and egocentric (e.g., head and body orientations) coordinate systems.[11,36–39] The heading estimates were systematically shifted when a reference was shifted. In Experiment 2, we asked participants to fixate on the display center and keep their eyes, heads, and bodies stable. Especially, eye-movement analysis showed that the fixation positions were not significantly different between left- and right-focus conditions. Therefore, ego-centric references were stable among different conditions. Experiment 2 showed that heading estimates were biased toward the focus of attention, suggesting that heading directions can be encoded with respect to the attention focus.

Moreover, previous studies have found that observers can use both egocentric and allocentric references to encode heading directions.[40] The neurons in the VIP cortical area represent the heading direction from optic flow, with respect to both egocentric and allocentric directions,[40] in an unconscious manner. In contrast, the attention-guided behavior in the current study is goal driven and conscious. Therefore, heading directions encoded with the reference to attention focus may differ from those encoded with reference to egocentric and allocentric centers.

Can neural model modulated by attention explain our attention effects?

Researchers have developed various neural models to understand the neural basis of heading perception, including the population heading map model,[41] the weighted spatial pooling model,[10] and the differential motion model.[42] These models generally propose that the final heading estimate is based on the direction of local motion vector summation in the flow field. Any change in the direction of the local flow vector summation will result in a change in the final heading estimate. However, our study found that the directions of the local motion vector summations did not significantly change in three experiments, regardless of the attention load or focus position. Therefore, these neural models could not explain the effects of attention on heading perception from optic flow.

Layton and Browning (2012)[43] developed a new neural model that consisted of two layers, similar to the weighted spatial pooling model.[10] Layer 1, working like the neurons in the MT area, contains many neurons and processes local vectors of optic flow. The activities of layer 1 are modulated by the attentional signal from the FEF area. Layer 2, working like the MSTd area, summarizes the inputs from MT area and decodes the FoE position. They found that their model well predicted the changes in MSTd area responding to FoEs in different attention states.

However, their models have two small potential issues. One issue is that Dubin and Duffy (2007, 2009)[17,18] developed "optic flow", which is non-optic flow.[36] As a result, it remains unclear whether the model is applicable to the optic flow in the current study. Another issue is that the model is based on the neural activities that mainly reflect the internal representation of heading directions. Heading estimates we collected in the current experiment were contaminated by motor response system or decision-making process. Xu, Sun, and Stocker (2023)[44] asked participants to estimate heading directions from optic flow. However, their responses could be constrained in a limited line/arc (e.g., Figure 1B) or freely in a circle. They found that headings were underestimated in the limited-line condition but overestimated in the circle condition, suggesting that heading estimates were different from internal representations. Therefore, it can be further examined whether Layton and Browning (2012)'s[43] model predicts the final estimates.

Limitations of the study

The current study uncovered the cognitive behavioral process that underlies the effects of attention on heading perception from optic flow. However, the neural basis remains unclear. Additionally, cognitive abilities are complex and contain various components, such as attention, working memory, learning, and decision-making. The current study only demonstrated the involvement of attention. Therefore, it remains unclear how the other types of cognitive abilities affect heading perception from optic flow and how they interact with each other. In summary, the current study opens several avenues for future studies.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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AUTHOR CONTRIBUTIONS

Conceptualization: Q.S.; data curation: Q.S. and L.Z.Z.; formal analysis: Q.S. and L.Z.Z.; funding acquisition: Q.S.; investigation: Q.S. and L.Z.Z.; methodology: Q.S.; project administration: Q.S.; resources: Q.S.; software: Q.S.; supervision: Q.S.; writing – original draft: Q.S. and L.Z.Z.; writing – review and editing: Q.S., L.Z.Z, F.H.Y., and X.F.D.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Cleaned data for all tasks	This paper	[Database]: [https://osf.io/fehcm/]
Software and algorithms		
Experimental code	This paper	[Database]: [https://osf.io/fehcm/]
MATLAB R2014b	MathWorks, USA	https://www.mathworks.com/products/matlab.html
Psychophysics Toolbox 3	http://psychtoolbox.org/	https://github.com/Psychtoolbox-3/Psychtoolbox-3/tree/3.0.19.2

RESOURCE AVAILABILITY

Lead contact

Further information and requests should be directed to the lead contact, Qi Sun (sunqi_psy@zjnu.edu.cn).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- The datasets from the current study have been deposited in a public repository. Database: https://osf.io/fehcm/.
- The data analysis codes and experimental program codes can be downloaded from https://osf.io/fehcm/.
- The idea and data were not disseminated before this manuscript.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

MODEL AND STUDY PARTICIPANT DETAILS

Participants

36 Chinese participants (Group 1: 10 males, 8 females; age: 18 – 23 years; Group 2: 7 males, 11 females; age: 19 – 29 years) were enrolled in Experiments 1a and 1b; 44 participants (Group 1: 6 males, 10 females; age: 18 – 23 years; Group 2: 8 males, 8 females; age: 18 – 25 years; Group 3: 5 males, 7 females; age: 18 – 23 years) were enrolled in Experiments 2a, 2b, and 2c; 15 participants (8 males,10 females; age: 18 – 24 years) were enrolled to conduct Experiment 3. All participants were with normal or correct-to-normal vision and were naive to the purpose of the experiment. The study was in accordance with the declaration of Helsinki and approved by the Scientific and Ethical Review Committee in the Department of Psychology of Zhejiang Normal university.

METHOD DETAILS

Stimulus and apparatus

Optic flow displays (Figure 1A, 80° H ×80° V) simulated observers translating at 4 m/s on a dot-ground (depth range: 0.20 – 5 m; eye-height: 0.17 m) consisting of 100 dots (diameter: 0.28°) (Figure 1A). The simulated heading direction of each display was randomly selected from ±28°, ±21°, ±14°, or ±7° in Experiments 1 and 2; that was randomly selected from 0° and ±21° in Experiment 3. Positive (negative) values meant that headings were right (left) to the display center (i.e., 0 degrees).

In some displays, three integers (RGB: [0, 0, 200]; 1.76° V × 1.76° H) were vertically presented on the display center (Figures 1B and 1C). The gap between the two numbers was 0.44°. In the perceptual and attention conditions of Experiment 1a, and the low-load condition of Experiment 1b, the first two numbers were randomly selected from the range [1, 10]; the third number was randomly selected from the range [1, 20]. In the high-load condition of Experiment 1b and the load condition of Experiment 3, the first two integers were randomly selected from the range [11, 40], and the third number was randomly selected from the range [40, 92].

Stimuli were programmed in MATLAB using the Psychophysics Toolbox 3 and presented on a 27-inch Dell monitor (resolution: 2560 H× 1440 V pixels; refresh rate: 60 Hz) with NVIDIA GeForce GTX 1660Ti graphics card.

Procedures

Preparation work of each experiment

All participants sat in a light-excluded room with their heads stabilized by a chin-rest. Participants viewed displays monocularly to reduce the conflict between motion parallax and binocular disparity depth cues. The viewing distance was 20 cm. Before starting the experiment, participants' straight-ahead direction was aligned with the display center indicated by a fixation point. Participants, therefore, were asked to fixate on the display center without moving their eyes throughout the experiment, removing the effects of eye movements on heading perception from optic flow.

Experiment 1

Experiment 1 consisted of Experiments 1a and 1b. Each sub-experiment included three blocks. Each block started with a fixation point on the display center. After participants clicked the left mouse button, the fixation point disappeared, and the trials started. The basic trial procedures in each block were similar. Specifically, on each trial, an optic flow display was first presented for 500 ms. After the optic flow display, a horizontal line appeared in the mid-section of a blank display. Participants were asked to move a mouse-controlled probe to indicate their heading estimate along the horizontal line. The position of the probe was randomly positioned on each trial. When participants clicked the mouse button, the next trial started.

In Experiment 1a, three blocks corresponded to the baseline, perceptual, and attention load conditions. The trial procedure in the baseline condition was the same as in the above trial illustration. The trial procedure in the perceptual load condition was similar to that in the baseline condition, except that each optic flow display contained three integers (Figure 1B). Participants were asked to ignore the numbers. The trial procedure in the attention load condition was similar to the perceptual condition, except that participants were asked to do a number-addition task before moving the probe to report their perceived headings. In the number-addition task, participants first summed the first two integers up and compared the sum with the third number. If the sum was smaller than the third number, then participants pressed the left arrow key; if larger, then pressed the right arrow key.

In Experiment 1b, three blocks corresponded to the baseline, low, and high attention load conditions. The trials of the baseline and low load conditions were the same as the baseline and attention conditions in Experiment 1a. The trials in the high load conditions were similar to that in the low load condition, except that the first two integers were randomly selected from the range [11, 40]; the third integer was randomly selected from the range [41 92]. The difficulty of the number addition task was increased.

Each block included 128 trials (8 headings × 16 trials). Before starting each block, participants were asked to conduct 10-15 practice trials randomly selected from the corresponding block. After the practice, the block started. In each sub-experiment, the conducting sequences of the three blocks were counter-balanced across participants. Each sub-experiment lasted for about 30 – 45 min.

Experiment 2

Experiment 2 included Experiments 2a, 2b, and 2c. Experiment 2a consisted of two blocks, corresponding to the baseline and center-focus conditions. In each trial of the center-focus condition (the 2nd row of Figure 3), five character-displays were sequentially presented. Each lasted for 150 ms, followed by a 50-ms blank display. The characters were randomly selected from B, E, N, Z, 6, and 9 and presented on the display center, which guided participants to focus on the display center. There were one or two numbers in the five displays. Once one number was presented, participants were asked to press the "SPACE" key as quickly as possible. A 200-ms optic flow display was randomly presented after the blank display of the 2nd, 3rd, or 4th character display. Randomly presenting the optic flow display could reduce participants' expectations and increase their attentional level. Participants were asked to report their heading estimates by moving a mouse-controlled probe on a horizontal line. The trial procedure of the baseline condition (1st row in Figure 3) was similar to that of the center-focus condition, except that all character displays were replaced with blank displays.

Experiment 2b included two blocks, corresponding to the baseline and left-focus condition. The trial procedures of the two conditions were the same as in Experiment 2b, but the character in the left-focus condition (the 3rd row in Figure 3) was left to the display center by 10°, which guided the focus of attention to the left side. It is noted that we propose the estimation errors induced by the left- and right-focus conditions were mirror symmetric. Therefore, only the left-focus condition was tested.

Experiment 2c also included two blocks, corresponding to the left- and right-focus condition. The trial procedures of the two conditions were the same as the corresponding conditions in Experiments 2a and 2b. Additionally, we also recorded the fixation positions of participants' right eye with Eyelink 1000 (SR Research, Ontario, Canada; sampling rate: 1000 Hz) to examine whether the heading bias shifted by the position of the attentional focus was due to the eye-movement.

Each block contained 128 trials (8 headings × 16 trials). Before the start of each block, participants were given 10-15 practice trials that were randomly selected from the experimental block. The conducting sequences of the two blocks in each sub-experiment were counter-balanced among participants. Participants took about 20 -30 min to finish the whole sub-experiment.

Experiment 3

Each participant completed a heading estimation task and a heading discrimination task. The procedure of the heading estimation task was similar to that of the baseline and high load conditions (hereafter referred to as the load condition) in Experiment 1b. Each heading was repeated 32 times, resulting in a total of 96 trials in each condition.

The discrimination task consisted of two blocks, corresponding to the baseline and load conditions. On each trial of the baseline condition, a 500 ms optic flow display was presented first. After the optic flow display, a blank display with a yellow vertical bar was presented. The position of the bar was 0°, 1.5°, 3°, 4.5°, 6°, 7.5°, 9°, or 10.5° to the left or right of the actual heading. Participants were asked to click the mouse button to indicate whether the bar was to the right or left of the actual heading. When the mouse button was clicked, the next trial started. The trial procedure of the load condition was similar to that of the baseline condition, except that two integers were presented in the center of the response display. Participants were asked to first compare the sum of the previous two integers with the third integer and press the left or right arrow key to indicate whether the sum was greater or less than the third integer. After pressing the key, they clicked the mouse button to indicate whether the bar was to the right or left of the actual heading. When the mouse button was clicked, the next trial started. Each block contained 540 trials (3 headings × 15 bar deviations × 12 trials).

Each participant conducted four blocks (2 blocks in the estimation tasks, and 2 blocks in the discrimination task). Before starting each block, participants completed 10-15 practice trials randomly selected from the experimental trials. The conducting sequence of the four blocks was counterbalanced among the participants. The whole experiment lasted for 1.5 hours.

QUANTIFICATION AND STATISTICAL ANALYSIS

Experiment 1

We first calculated the accuracies of the number addition task to examine whether participants followed experimental instructions. We removed the participants if their accuracies were below 75%. As a result, 18 and 17 effective data were kept in Experiments 1a and 1b. Additionally, in Experiment 1b, the accuracy of the low-load condition (Mean $\pm$ SD: 0.97 $\pm$ 0.017) was significantly higher than that of the high-load condition (0.93 $\pm$ 0.036) ($t(16) = 6.42$, $p < 0.001$), suggesting that the high load condition was more difficult than the low load condition.

The heading estimates were recorded in the experiments. Previous studies have shown that headings from optic flow are systematically compressed towards the display center (0°),[8,10,11] leading to that the heading estimates were smaller than the actual headings. The smaller the heading estimates, the lower the estimation accuracies. For each sub-experiment, we conducted a 3 (experimental conditions) × 8 (headings) repeated measures ANOVA on heading estimates to test whether experimental conditions affected heading estimation from optic flow. If there was a significant interaction between experimental conditions and headings, Newman-Keuls post hoc analysis was conducted to test the differences in perceived headings among different experimental conditions in each heading.

Experiment 2

To examine whether the focus of attention affected heading estimation, we calculated the normalized estimation difference (NED) in each heading, given by Equation 1.

In which, HE_{focus} was the heading estimate of the center-focus condition (Experiment 2a) or the left-focus condition (Experiment 2b). $HE_{baseline}$ was the heading estimate of the baseline condition (Experiments 2a or 2b). A 2 (focus positions: center vs. left) × 8 (headings) mixed-repeated measures ANOVA on the NED was conducted to examine whether the focus positions had effects on heading estimation from optic flow.

To uncover whether the attention was covert or overt, we recorded eye-movements in the left- and right-focus conditions. A 2 (focus positions: right vs. left) × 8 (headings) repeated measures ANOVA was conducted on the horizontal and vertical position of fixations. If the main effect of focus positions was not significant, then attention was covert.

Experiment 3

The accuracies of the number addition task of all participants were beyond 0.75.

For the discrimination task, we calculated the proportion of right responses (PRR) of each bar deviation (0°, 1.5°, 3°, 4.5°, 6°, 7.5°, 9°, or 10.5°) in each actual heading. Then, we fitted the PRR as a cumulative Gaussian function of the bar position (BP, the sum between the bar deviation and the actual heading) for each actual heading, given by:

In which, μ corresponds to the point of subjective equality (PSE); σ indicates the standard deviation of the cumulative Gaussian curve, which is proportional to the discrimination threshold. Large σ indicates high discrimination threshold, indicating a low precision of the internal representation.

To examine whether the attention load affected heading discrimination, one 2 (experimental conditions: baseline vs. load) × 3 (headings) repeated measures ANOVA was conducted on the σ.