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Brief communication

An illusory transformation of optic flow fields without local motion interactions

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Abstract

The focus of expansion (FOE) of a radially expanding optic flow pattern that is overlapped by unidirectional laminar flow is perceptually displaced in the direction of that laminar flow. There is continuing debate on whether this effect is due to local or global motion interactions. Here, we show psychophysically that under conditions without local motion transparency the illusion becomes weaker but can still be observed. In our experiments, the radial and laminar-flow fields were not presented with overlap but separately to the left and right halves of the visual field with a blank vertical strip of 15° horizontal width in between. The illusory shift observed in this condition cannot be explained by local motion interactions because (a) no transparent motion was present in the stimulus, and (b) the receptive fields of cortical cells involved in the analysis of local motion cross the vertical midline of the visual field to a limited extent. We conclude that global motion detectors that integrate motion from both halves of the visual field play a role in shifting the perceived position of the FOE and that local motion interactions may be sufficient, but are not necessary for the optic flow illusion to occur.

Keywords: Optic flow; Heading; Illusion; Visual psychophysics

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1. Introduction

When a radially expanding optic flow pattern is overlapped by unidirectional laminar flow, the focus of expansion (FOE) is perceptually displaced in the direction of that laminar flow. This phenomenon is known as the optic flow illusion (OFI), which was first described by Duffy and Wurtz (1993). They hypothesized that the visual system interprets the laminar flow as a reafferent stimulus indicating an eye movement. The OFI would then result from an attempt of the visual system to compensate for the distorting effect a real eye movement would have had on the flow field (Pack & Mingolla, 1998). The OFI has also been related to local motion induction, illusory motion of a visual stimulus opposite to the real motion of abutting stimuli (Meese, Smith, & Harris, 1995). This type of motion induction is attributed to antagonistic interactions of adjacent or concentric excitatory and inhibitory regions within the receptive fields of motion-sensitive neurons, also known as center–surround interactions (Anstis & Reinhardt-Rutland, 1976).

Recently, debate has risen on whether the OFI is caused by a global eye rotation compensation mechanism or by local motion interactions. Royden and Conti (2003) showed that a neurobiologically motivated implementation of a vector subtraction model (Longuet-Higgins & Prazdny, 1980; Rieger & Lawton, 1985) could predict the direction and magnitude of the illusory shift. The computational operators of this model had properties similar to cells found in the middle temporal area (MT) of the macaque visual cortex, which are direction

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selective and often center–surround organized. Furthermore, they showed that the focus shift also occurs when the expanding pattern is overlapped by a second expansion flow, instead of laminar flow. This focus shift was found both for human observers and in the local motion subtraction model. Royden and Conti (2003) reasoned that, since this bifocal flow cannot result from eye movements, the illusory shift in this situation is not prone to the eye rotation compensation account by Duffy and Wurtz. They concluded that the local motion interactions are crucial to explain the OFI.

However, Hanada (2005) recently showed computationally, that both the radial + laminar and the bifocal flow could be regarded as special cases of rigid motion flow, i.e., flow due to observer movements in a stationary scene. He claimed that any model that can compensate for the effect of eye movements on flow fields would exhibit behavior that at least qualitatively corresponds to the OFI in humans. In this view, local motion interactions are unnecessary for the OFI to occur.

Here, we present psychophysical data in support of the latter view. In our OFI experiments, the planar and radial fields were not presented with overlap but separately to the left and right halves of the visual field with a blank vertical strip of 15° horizontal width in between. These conditions minimize the possibility of local center–surround interactions in MT cells because (a) no transparent motion was present in the stimulus, and (b) the receptive fields of MT cells typically extend only a few degrees beyond the vertical midline of the visual field in macaque (Desimone & Ungerleider, 1986; Van Essen, Maunsell, & Bixby, 1981) and humans (Dukelow et al., 2001; Huk, Dougherty, & Heeger, 2002). In the seven subjects that participated in our experiments, the illusion became much weaker than in a reproduction of the original full field experiment by Duffy and Wurtz (1993), however, it could still be observed. This result indicates that the OFI can occur in the absence of local motion interactions, and that the integration of motion from both halves of the visual field plays a role in shifting the perceived position of the FOE.

2. Methods

2.1. Subjects

Seven male subjects, who were 21 to 47 years old, with normal or corrected to normal vision, participated in this study. Three were completely naive as to the hypothesis under study (E.P., R.S., and W.H.). The authors (J.D., J.B., R.W., and A.B.) also participated in the experiments. Two (J.B. and A.B.) had extensive experience with optic flow displays. All subjects had participated in other types of psychophysical experiments prior to the ones presented here.

2.2. Visual stimuli

Visual stimuli (Fig. 1) were generated with OpenGL on an Apple PowerMac G4 (1 GHz) and back projected onto a translucent screen with a JVC DLA-S10 beamer at 75 frames/s. The display subtended 105° × 77° at a viewing distance of 58 cm. The stimuli were two animations of optic flow resulting from two independently simulated observer movements through two artificial environments of dots. One animation was a radial expansion flow resulting from a simulated 2 m/s ap-

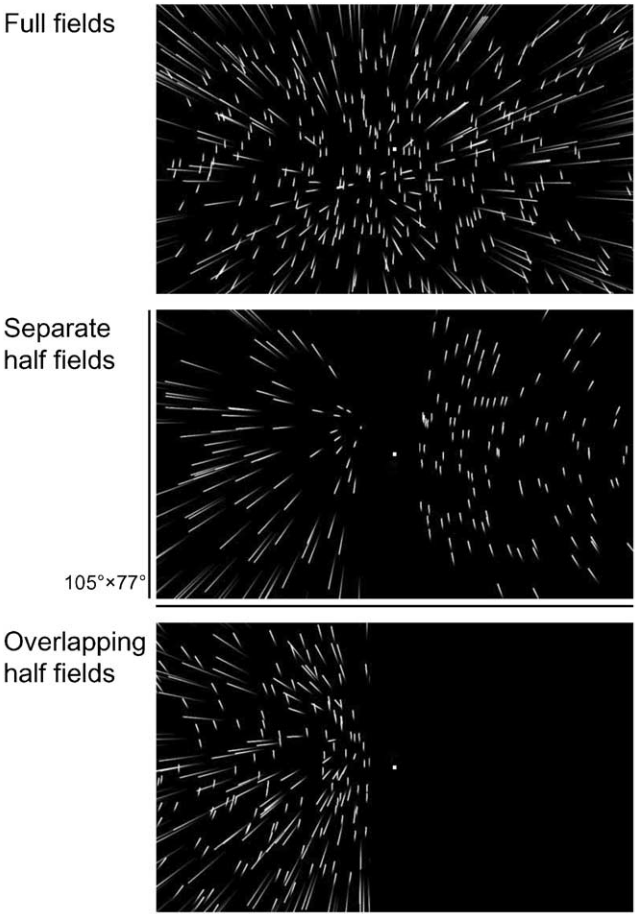

Fig. 1. Stimuli consisted of two transparent flow fields: a radial flow, resulting from simulated forward heading, and a laminar flow, resulting from simulated rotation around a horizontal axis. In the *full fields* condition, these flow fields were shown entirely. In the *separate half-field* condition, the flow fields were partly occluded such that only the left half of the radial, and the right half laminar flow were visible. This stimulus contained no transparent motion. In the *overlapping half-field* condition, the right halves of both flow fields were occluded. In both half-field conditions, the central 15° were additionally occluded. A red fixation dot was always present in the center of the screen. Each of the images in this figure is a superposition of all 75 frames of a one second trial. (To disambiguate motion directions, the luminance of each frame's dots is scaled as a function of frame number. For visibility, the fixation dot size has been scaled by a factor 3.) Note that the hyperbolic trajectories of the laminar-flow fields made that—from the vantage point of the observer—the flow had a constant velocity across the display.

proach toward a fronto-parallel plane of dots. This plane was situated at 15 m from the observer at the onset of each trial. The simulated observer translation was directed at 10° to the left of the observer's straight ahead. Vertically, one of 21 directions was picked randomly among trials, ranging from ±10°. The other animation depicted the laminar flow that would result from a 4 deg/s rotation around a horizontal axis through the observer's eye in a sphere of dots. This sphere was centered on the vantage point of the observer and had a radius of 5 m. The total number of dots on its surface was 1240 (0.03 dots/deg^2). Three different experiments were done. In the first experiment, both animations covered the entire display area and were transparently superimposed, similar to the experiment of Duffy and Wurtz (1993). We called this the *full fields* condition. In our second experiment, only the right half of the laminar flow and the left half of the radial flow were displayed. This was the *separate half-field* condition. Finally, in the third experiment (called the *overlapping half-field* condition), only the left halves of both animations were visible. Both half-field conditions had an additional blank vertical strip that occluded the central 15° of the optic flow stimuli. In the full fields experiment, both transparent flow patterns consisted of 250 dots on average per trial. In the half-field experiments, the mean number of visible dots was 108 for the radial and 114 for the laminar flow. Dots had a diameter of 3 pixels (corresponding to .27° foveally) and were rendered using OpenGL's anti-aliasing to get smooth animation. Dot color was white (46.4 cd/m^2). The luminance of the dark background was .11 cd/m^2 during the animations. In between animation intervals, the background luminance was 4.78 cd/m^2.

2.3. Experimental procedure

Subjects were seated in a room with no lighting other than the projector. Their right eyes were occluded and their left eyes were exactly in front of, and 58 cm away from, the center of the screen. In this position, which was maintained by means of a biteboard, all edges of the display were visible while the subjects fixated a red fixation dot in the center on the screen. Each subject participated first in the full-field, then in the separate half-field, and finally in the overlapping half-field experiments. Each experiment, consisting of 10 blocks of 63 trials, either lasted 40 min or was completed in two 20 min sessions. At the beginning of each experiment, the participants were familiarized with the stimulus and the task by performing a number of practice trials.

Each trial consisted of an animation and a pointing phase, the onsets of which were accompanied by different auditory cues. A trial started with the animation phase in which the two optic flow displays were simultaneously shown. The subjects were instructed to locate the focus of the radial expansion. After one second, the animation stopped and the dots remained static on the screen. At the same time, the background luminance was increased from .11 to 4.78 cd/m^2 to prevent luminance aftereffects of the trajectories of the slowly moving dots that would otherwise have indicated the veridical FOE position. In this static period, a horizontal line spanning the width of the display appeared in the center of the screen. Subjects had to vertically align this line with the perceived FOE location by means of a mouse. After this, the participants could start the next trial by clicking the mouse. Subjects were instructed to maintain fixation throughout both the animation and the pointing phases.

3. Results

Fig. 2 shows the responses of one subject in the full field and both half-field experiments. In these scatter plots, the perceived FOE location is shown as a function of the veridical FOE location with each point representing the result of one trial. Different symbols are used to indicate what kind of inducing stimulus was present during the trial: ±4 deg/s laminar flow or static dots. These data were analyzed by fitting a plane according to the following multiple linear regression model: $Y_{\mathrm{perc}} = \alpha + \beta Y_{\mathrm{real}} + \gamma V_{\mathrm{lam}}$. Here, Y_{perc} is the perceived vertical position of the FOE, Y_{real} is the real vertical FOE position, and V_{lam} is the velocity of the laminar flow. In Fig. 2, three intersections of this plane at the V_{lam} values of −4, 0, and 4 deg/s are shown. Values of γ that are significantly greater than zero indicate that the perceived focus was shifted in the direction of the laminar flow: the OFI had occurred. The perceptual displacement for a laminar-flow condition equals the laminar-flow velocity in deg/s multiplied by γ. These values are shown in Fig. 3A for every subject in each of the three experimental conditions (full-field, separate half-field, and overlapping half-field). The largest illusory effects were found when the flow fields covered the entire screen. However, in the separate half-field experiments, a significant displacement of the perceived FOE position from the true FOE position could still be observed in all subjects ($p < .05$). Mean shift (Fig. 3B) in this condition was 17% of the shift observed in the full fields condition. The overlapping half-field experiments, in which the two half-field stimuli were both presented to the left of the vertical meridian of the visual field yielded an illusory shift of, on average, 61% compared to the full fields condition.

4. Discussion

The computational study by Hanada (2005) showed that the mechanism of center–surround motion interaction

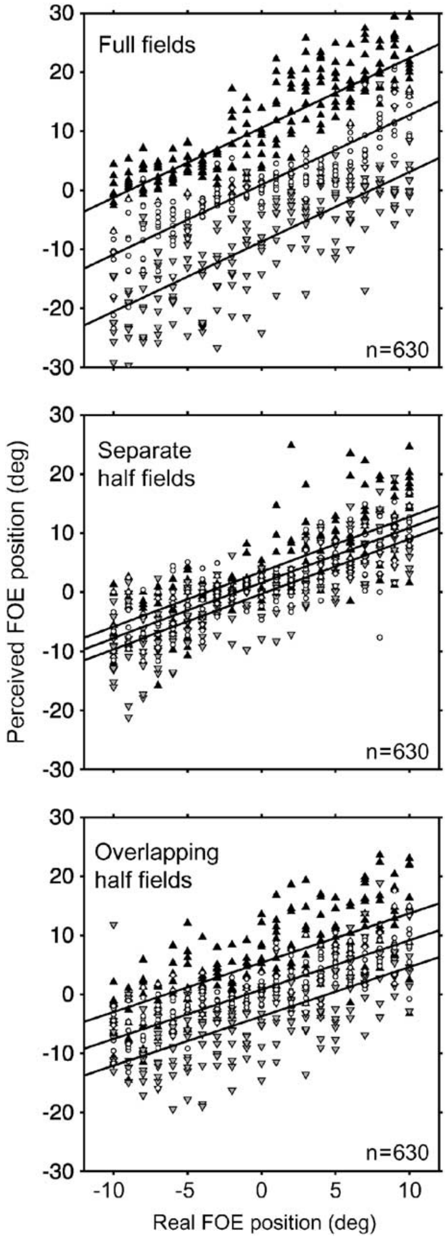

Fig. 2. Data of one subject (E.P.). Each scatter plot pairs the real and perceived focus of expansion positions for three different stimulus conditions: full field, separate half-field, and overlapping half-field. A laminar-flow pattern moved at a speed of 4 deg/s upward (▲) or downward (▽), or a static pattern was shown (○). The data of all 630 trials per experiment were fitted with a plane in the volume perceived-focus-position × real-focus-position × laminar-flow-velocity. The three lines in each graph are intersections of this plane at the three laminar-flow speeds used (−4, 0, and 4 deg/s). The offsets of these lines indicate that, in all stimulus conditions, the FOE was perceptually displaced in the direction of the laminar flow.

is not required to explain the OFI. However, as noted by Hanada (2005), this analysis does not exclude the motion subtraction explanation of Royden and Conti (2003). Here, we tested the hypothesis that the OFI does not result from local motion interactions alone.

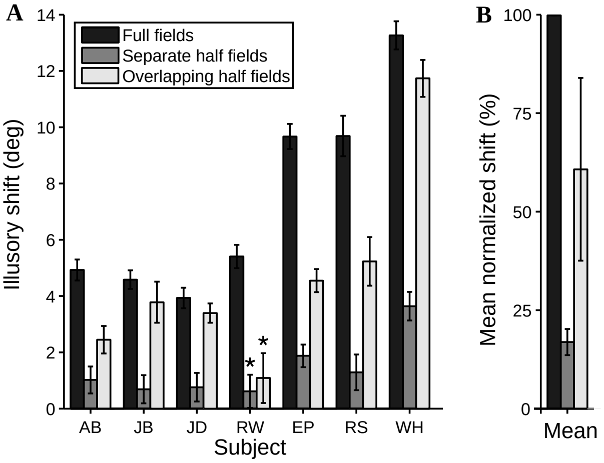

Fig. 3. (A) The illusory shift observed in seven subjects in the full fields, separate half-field, and overlapping half-field conditions. These values and their 95% confidence intervals were obtained by multiple linear regression. All shifts were statistically significant ($p < .01$, except where indicated by a $*$, $p < .05$; $n = 630$). (B) Mean shifts of all subjects, normalized to each subject's full fields OFI magnitude. The OFI magnitude observed in the separate half-field conditions was the smallest, 17% compared to the full fields condition. The overlapping half-field conditions yielded 61%. (Error bars are 95% confidence intervals, $n = 7$.)

In the full fields experiment, we reproduced the finding by Duffy and Wurtz (1993) that the focus of a full field expansion pattern is shifted in the direction of overlapping full field laminar flow—the direction of which was vertical in our experiments, instead of horizontal in all previous psychophysical OFI studies (Duffy & Wurtz, 1993; Grigo & Lappe, 1998; Meese et al., 1995; Royden & Conti, 2003). The separated half-field experiments was designed to minimize the possible effects of local motion interactions: the expanding and laminar flow fields were presented separately to the left and right halves of the visual field. In agreement with our hypothesis, the OFI could still be observed in all subjects, albeit to a much smaller extent (mean magnitude: 17% of shift in full fields condition). The overlapping half-field conditions was a control to test whether the reduction in OFI magnitude resulted not from the reduction of local motion interactions per se, but from the reduction of total motion energy in the stimulus, i.e., the reduction of the total number of moving dots. Here, the two flow fields were projected onto the same half of visual field. The OFI in this condition was a factor 3.6 larger than in the separate half-field conditions. This control experiment suggests that local motion interactions do play an important role in the OFI. It should be noted, however, that the difference between the two half-field conditions might have been facilitated by attentional effects. In the separate half-field conditions, the observer has to locate the FOE in the left half of his visual field. The laminar flow presented to the right could be ignored, potentially reducing its effectiveness as an OFI inducer.

These findings are similar to those of Pack and Mingolla (1998) who showed that the magnitude of the OFI continued to increase when the laminar-flow field extended beyond the edges of the expansion field. However, it has been suggested that the size effect found by Pack and Mingolla (1998) may still be attributable to center–surround motion interactions (Royden & Conti, 2003), because of the finding that motion sensitive cells have large surrounds, especially at the large eccentricities used in their experiment. This argument is less applicable to the result presented here, because the receptive fields of motion-sensitive cells cross the vertical midline of the visual field that separated the two flow fields in our experiment to a limited extent.

Although the results of Pack and Mingolla (1998) and our experiments show that the OFI comes at least partially about by motion interactions beyond the range of what is normally considered local (i.e., $\geqslant 15^\circ$ in our experiments), we cannot exclude that center–surround motion subtraction might be the functional mechanism, but then operating at a very large scale. Cells in motion-sensitive cortical areas MST are known to have large receptive fields that reach well beyond the vertical midline of the visual field (Duffy & Wurtz, 1991a; Raiguel et al., 1997). To our knowledge, however, it is unknown whether these cells have an appropriate center–surround structure to explain the OFI by this mechanism. In addition, it is unclear to us whether a center–surround motion subtraction model such as the one of Royden and Conti (2003) is likely to predict the OFI when presented with our separate half-field stimuli using operators of this scale.

Large-scale flow detectors are used by several physiologically inspired models of heading detection that explicitly address eye rotation detection from visual cues (Beintema & van den Berg, 1998; Lappe & Rauschecker, 1994, 1995; Perrone & Stone, 1994). The global eye rotation detection in these models might explain the integration of motion from both halves of the visual field that gives rise to the OFI observed in all subjects in our separate half-field experiments. The data presented here are in line with the original Duffy and Wurtz (1993) explanation of the OFI, being that global laminar flow triggers the visual system to compensate for eye rotation. However, it should be noted that our experiments were not designed to explicitly test this idea.

Our experiments suggest that local motion detectors play a role in the OFI, considering the robust shifts of the FOE observed in the full fields and overlapping half-field conditions. However, we conclude that global motion detectors are sufficient for the OFI to occur because the shift could still be observed in the separate half-field experiments lacking local motion transparency.

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