Spatial distortions produced by purely dichoptic-based visual motion

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Received 19 September 2008, in revised form 24 October 2008; published online 18 May 2009

Abstract. It is known that local, monocular motion (short-range motion) can produce local distortions of visual space. We wanted to know if local monocular motion was both sufficient and necessary for producing motion-based spatial distortions. We used a previously reported dichoptic motion stimulus in which the directional motion signal is not present in either eye’s input but is only present after binocular combination. We show that such a stimulus can also induce perceived changes in spatial position. This suggests that local, monocular motion while being sufficient is not necessary for the production of motion-based illusions. It suggests that one source of motion signals responsible for this illusion is from binocular motion mechanisms.

1 Introduction
Our ability to estimate the position of an object depends on whether its surface markings are static or in motion (Anstis 1989; Ramachandran and Anstis 1990). This was shown in a simple 3-element alignment task comprising 1-D Gabor stimuli by De Valois and De Valois (1991). If the middle Gabor has a moving carrier and stationary envelope, its overall position is perceived to be shifted in the direction of the motion. The same perceived distortion occurs following adaptation to visual motion (Nishida and Johnston 1999; Snowden 1998). Single-unit recording in cats has shown that cells in early visual areas exhibit positional shifts of their receptive fields during local image motion (Fu et al 2004), and functional imaging studies in man (Whitney et al 2003; Whitney and Bressler 2007) have found evidence for changes in the retinotopy within early visual areas during local image motion. This information suggests that cells in early visual areas are involved in this perceptual phenomenon, but it is not known whether it is a local effect confined to early visual areas or one that occurs as the result of feedback from higher visual areas. There is some support for the latter from TMS (McGraw et al 2004) and psychophysical studies (McGraw et al 2002), based on indirect evidence (the lack of stimulus specificity).

It is well accepted that motion perception is not a single process. This argument originates from Braddick’s dual-process theory, where short-range and long-range motion systems are assumed (Braddick 1974). The short-range motion system is sensitive to short distance displacements and rapid temporal changes, whereas the long-range motion system is responsible for detecting large displacements of features. A more modern classification of motion sub-systems involves first-order, second-order and feature tracking (Cavanagh and Mather 1989). Although it is still uncertain if the original long-range category maps onto the more modern second-order category, there is good agreement that short-range and first-order motions are synonymous. There is psychophysical evidence that short-range motion mechanisms, thought to reside in lower visual

(1) Neurophysiology and brain-imaging studies showed that the distribution of response shifted opposite to the direction of motion (Fu et al 2004; Whitney et al 2003; Whitney and Bressler 2007). This is a reverse to the results of psychophysical studies, where the perceived position of motion stimuli was found to be shifted in the direction of motion (De Valois and De Valois 1991; Nishida and Johnston 1999; Ramachandran and Anstis 1990; Snowden 1998; Whitaker et al 1999).
areas (e.g., V1) are essentially monocular (Georgeson and Shackleton 1989, 1992; but also see Carney and Shadlen 1993). However, motion-responsive neurons in many visual areas (V1, MT, and MST) are known to be binocular.

Shadlen and Carney (1986) found that, if a moving sinusoidal grating was decomposed into two flickering gratings in spatiotemporal quadrature and presented to each eye, subjects could perceive the motion direction. Since such motion is not present in the monocular images (each sees a counterphasing stimulus), it represents a cyclopean motion phenomenon. They interpreted the illusion as a result of the short-range motion system occurring after binocular integration. In principle, it could have been the result of low-level binocular motion-energy detectors or higher-level motion feature-trackers. A recent report (Hayashi et al. 2008) suggests the former, as a similar binocular motion phenomenon can be demonstrated with featureless stimuli. We wanted to know if such a motion stimulus induced spatial distortions. If it does, then it would suggest that motion-based spatial distortions are not exclusively driven by low-level monocular motion mechanisms and can occur as a result of motion signals at or after binocular integration.

In this study we measured positional sensitivity using a standard 3-element alignment task in which the central element contained either local (binocular) or cyclopean (dichoptic) motion. Our results show that dichoptic motion also induces positional shifts, suggesting that local monocular motion is sufficient but not necessary for producing motion-based spatial distortions. Signals from purely binocular motion units can also produce comparable distortions. We also found the amount of motion-induced positional shift was related to the strength of perceived binocular motion, suggesting the strength of the motion signal is related to the extent of spatial distortion.

2 Methods

2.1 Observers
Seven observers (including the authors) with normal or corrected-to-normal vision participated in the experiment. They all volunteered to perform the task. Observers were staff members at McGill Vision Research.

2.2 Apparatus
The stimuli were presented on COMPAQ P1210 CRT monitor controlled by the VSG2/5 graphics board (Cambridge Research Systems) with 15 bits of contrast resolution, housed in a Pentium PC computer. The screen resolution was 1024 × 768 pixels with frame rate of 120 Hz and mean luminance of 37 cd m⁻². Observers looked at the stimuli through a mirror stereoscope. Viewing distance was 57 cm.

2.3 Stimuli
There were two types of motion stimuli: dichoptic and binocular. Dichoptic motion stimuli were composed of a pair of Gaussian-windowed vertical sinusoidal gratings (Gabor patterns) with a spatial frequency of 1.5 cycles deg⁻¹ and Michelson contrast of 0.3. The standard deviation of the Gaussian window function was 1 deg of visual angle. Each Gabor pattern flickered with a rate of 4 Hz and presented to the left or right eyes. This configuration could yield motion in cyclopean view. The intensity profiles of the underlying gratings for the left and right eyes (L_L and L_R) can be defined as a product of spatial and temporal sinusoidal modulation:

\[ L_L(x, t) = L_0 [1 + c \cos(f x) \cos(\omega t)] , \]  \hspace{1cm} (1)

and

\[ L_R(x, t) = L_0 [1 + c \sin(f x) \sin(\omega t)] , \]  \hspace{1cm} (2)
where $L_0$ is mean luminance, $c$ is the Michelson contrast of the grating, and $f$ and $\omega$ respectively represent spatial and temporal frequencies. The substitution of $\sin$ for $\cos$ in equation (2) means a quarter cycle difference in space and time. The sum of left and right intensity profiles is a drifting grating:

$$L_L(x, t) + L_R(x, t) = L_0[2 + c \cos(fx - \omega t)].$$

(3)

Binocular motion stimuli were drifting Gabor patterns presented to both eyes. Their intensity profile was the same as that of the fused dichoptic motion stimuli [equation (3)].

We presented the reference stimuli to both eyes, at 2 deg above and below the motion stimuli. The reference stimuli were flickering Gabors with the same spatial patterns as described in equation (2). The sine phase of the reference stimuli was 0° or 180° (counter-phasing) at the horizontal centre of the stimulus field.

Crosshairs consisting of four thin short lines were always presented, to indicate the centre of the stimulus field and to confirm precise binocular alignment. The two orthogonal lines were present at the top-left and bottom-right portions of the stimulus field in one eye, while another two lines were present at the top-right and bottom-left portions in the other eye. Experiments started after confirming that the four lines look as an ‘X’ symbol without the cross in the centre.

2.4 Procedure

Observers judged whether the positions of the motion stimuli were displaced to the right or to the left of the reference stimuli. The dichoptic motion stimuli and reference stimuli were presented for 1 s. A tone indicated the beginning of each trial.

The independent variables were motion type (dichoptic or binocular) motion direction (leftward or rightward), and a horizontal positional shift of the motion stimuli. There were nine levels of the positional shift (visual angles of $-7.2$, $-5.4$, $-3.6$, $-1.8$, 0, 1.8, 3.6, 5.4, and 7.2 min of arc). At least twenty trials were devoted to each condition. That is, an experiment consisted of more than 720 ($2 \times 2 \times 9 \times 20$) trials. The trials were randomised.

3 Results

Figure 1 shows probabilities of perceiving leftward positional shift against the physical location of the motion stimuli. For the binocular motion condition, the direction of motion influences the positional judgment which is consistent with other studies (De Valois and De Valois 1991; McGraw et al 2002). The magnitude of the positional shift varied between subjects for both the binocular motion and the dichoptic motion stimuli (figure 2). For most of the subjects, a motion-induced positional shift was present but was smaller for dichoptic motion.

Cumulative normal functions were fitted to the data by a bootstrap procedure (Wichmann and Hill 2001a, 2001b). Here, we use their $z$ values (means of the cumulative normal functions) as index of the perceived positional shifts. An $z$ value represents a physical position which produces a $0.5$ probability of perceiving leftward shift. Although there is some variation across subjects, it is clear that dichoptic motion, like its binocular counterpart, can induce significant shifts in perceived spatial position.

We measured performance for motion-direction discrimination. The correct rates ranged from 0.51 to 0.98 for dichoptic motion stimuli, whereas observers could almost perfectly discriminate direction of binocular motion stimuli. That is, perceptually, there was a difference in the quality of motion between the dichoptic and binocular motion stimuli. The strength of the motion percept is much weaker in the former case and direction discrimination is often below the ceiling values typical of binocular motion. We wondered if this weaker motion percept could explain why some subjects displayed smaller positional shifts for the dichoptic compared with the binocular motion stimulus.
In order to assess the relationship between the magnitude of positional shift and perception of motion, we plotted a distribution of the correct rates and positional shift index for dichoptic motion stimuli (figure 3). The positional shift index $I_{\text{shift}}$ is defined by the following equation:

$$I_{\text{shift}} = \frac{\alpha_{\text{RD}} - \alpha_{\text{LD}}}{\alpha_{\text{RM}} - \alpha_{\text{LM}}}$$  (4)

**Figure 1.** Differences in a horizontal positional shift between binocular (black) and dichoptic (grey) motion stimuli. Each point shows a probability of perceiving leftward positional shift against the physical location of the motion stimuli. Circle and square symbols correspond to the leftward (L) and rightward (R) direction conditions, respectively. Curves are the fitted cumulated normal functions and horizontal thin lines are the standard deviations of the fits.
where $\alpha_{ij}$ is an $\alpha$ value for dichoptic or binocular motion stimuli ($j$) drifting rightward or leftward ($i$). If the positional shift index equals 1, there is no difference in the positional shift between dichoptic and binocular motion stimuli. The lower the positional shift index is, the larger the difference becomes. We can see from figure 3 that the dichoptic motion stimuli could produce a substantial positional shift if observers had a strong sense of motion direction. The data show a trend suggesting a correlation, although it is not statistically significant, for the number of subjects tested.

**Figure 2.** Horizontal positional shifts for dichoptic and binocular motion stimuli drifting rightward (R) or leftward (L). We used $\alpha$ values (means of the fitted cumulative normal functions) as an index of positional shifts.

**Figure 3.** The distribution of the positional shift index, $I_{\text{shift}}$, and correct rates of motion direction discrimination for dichoptic motion stimuli.

### 4 Discussion and conclusions
We show here that stimuli that do not produce any percept of motion in each eye’s input can result in a motion-induced distortion of visual space if this information is integrated within binocular motion detectors. This suggests that local monocular motion is sufficient but not necessary for producing motion-induced distortions of visual space, because motion signals carried by units with binocular properties can produce distortions of space also. This is consistent with McGraw et al’s (2002) finding that
the motion aftereffect (MAE) produces a positional shift not only in the adapted eye, but also in the non-adapted eye. Our results do not directly bear upon the controversy whether the short-range motion processing is fundamentally monocular in nature (Georgeson and Shackleton 1989, 1992) or not (Carney and Shadlen 1993), because it is unresolved if the mechanisms for motion-induced spatial distortions are the same or different from those carrying short-range motion signals. Our findings show that this dichoptic motion, like its monocular counterpart, can induce perceptual shifts in position.

We also found that the strength of the motion percept affects the extent of the spatial distortion induced by the dichoptic motion stimuli. There is a controversy whether motion perception is necessary for motion-induced spatial distortions (Watanabe 2005) or not (McGraw et al. 2002). This controversy originates from the use of different motion stimuli. Watanabe (2005) and the present study used real motion to induce a positional shift, whereas the MAE was used in McGraw et al.’s (2002) experiments. The latter found that the MAE-induced positional shift remains relatively constant despite differences in stimulus features (orientation, spatial frequency, and so on) between adapting and testing stimuli, and noted that this characteristic is very different from that of the traditional MAE. We speculate that MAE-induced positional shifts result from adaptation to a positional shift, rather than to motion per se. Thus motion perception may not be necessary for the MAE-induced positional shift.

The present results do not bear directly upon the physiological nature of the mechanism underlying motion-induced spatial distortions. We know from single-unit studies (Fu et al. 2004) that V1 cells, specifically complex cells, exhibit shifts in their receptive field position (though in the opposite direction to that of the psychophysics) contingent upon visual motion. These cells have properties that would make them possible candidates for binocular motion processing (Hayashi et al. 2008; Qian and Andersen 1997). There would then be no need to postulate feedback from higher visual areas such as MT or MST. On the other hand, TMS studies (McGraw et al. 2004) have suggested that higher motion areas may be involved, because the effects of prior adaptation to motion on perceived spatial location can be disrupted by applying TMS to area V5/MT (as opposed to area V1). This led to the suggestion that the site of interaction may be in area MT rather than area V1. This would also be consistent with our results, depending on whether the site of binocular motion processing is in V1 or MT.

Acknowledgment. This work was supported by an NSERC grant (41528-06) to RFH.

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