Eye-specific information biases perceived direction of bistable motion

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While eye-of-origin information is normally not accessible to observers, processing of visual information within a monocular channel does contribute to our final percept. Here we investigate if visual information is processed more efficiently when it is contained within a monocular channel or across two eyes and how it affects visual perception. Specifically, we used a bistable apparent motion display, a motion quartet, to investigate the role of eye-specific information in determining perceived motion direction. To an observer, this ambiguous display leads to the perception of either horizontal or vertical motion. We attempted to bias perceived direction by presenting separate spatial halves of the motion quartet to each eye. Our results show that observers were more likely to see horizontal motion when top and bottom halves of the quartet was presented to separate eyes. Similarly, when left and right halves were presented dichoptically, observers reported viewing more vertical motion. This change in proportion of observed motion direction indicates that eye specific information is processed more efficiently and can bias overall perception.

Introduction

It is known that visual inputs are processed both monocularly and binocularly. A unique feature of early visual areas such as V1 and the lateral geniculate nucleus (LGN) is that information is segregated based on eye-of origin (Connolly & Van Essen, 1984; Horton, Dagi, McCrane, & de Monasterio, 1990). This distinction is not present in extrastriate areas, which do not discriminate between signals originating from either eye (Dubner & Zeki, 1971; Watson et al., 1993; Zeki et al., 1991). In V1, there are neurons that preferentially respond to information originating from the left or right eye arranged alternately in ocular dominance columns (Horton et al., 1990; Shmuel, Chaimow, Raddatz, Ugurbil, & Yacoub, 2010). Similarly, in the LGN, visual information originating from each eye is kept in distinct monocular layers (Connolly & Van Essen, 1984). Even though eye-of-origin information is preserved during initial stages of visual processing, this information appears not readily available to our awareness. Whether visual stimuli are processed more efficiently when they are presented monocularly (in the same eye) than presented binocularly (across the two eyes) remains unclear too.

On the one hand, it is generally agreed that two eyes are better than one. Binocular advantage has been demonstrated across a multitude of tasks such as depth perception, contrast sensitivity, vernier acuity, color and letter discrimination (Banton & Levi, 1991; Blake, Sloane, & Fox, 1981; Jones & Lee, 1981; Wheatstone, 1838). Moreover, we are typically quite poor in discriminating with which eye a visual stimulus originates (i.e., utrocular discrimination) except for visual stimuli with low spatial frequencies (Blake & Cormack, 1979; Martens, Blake, Sloane, & Cormack, 1981; Ono & Barbeito, 1985; Schwarzkopf, Schindler, & Rees, 2010). This inability would suggest that we do not have much preference towards information contained within a monocular channel. Thus, it would seem unlikely that visual stimuli will be processed more efficiently when they are presented monocularly.

On the other hand, it has been recently demonstrated that processing within a specific monocular channel can be modulated by voluntary attention to alter stimulus strength during binocular rivalry (Ooi & He, 1999; Zhang, Jiang, & He, 2012), suggesting that information within a specific monocular channel may be processed together to bias perception.

To directly test whether visual stimuli are processed more efficiently when they are presented monocularly, here we study the relative strengths of monocularly and binocularly presented stimuli.
dichoptically presented long-range apparent motion behaviorally with a bistable motion quartet paradigm. The motion quartet is a variant form of the apparent motion illusion (Anstis & Ramachandran, 1987; Ramachandran & Anstis, 1985). An intriguing feature of a bistable visual stimulus such as the motion quartet is its ability to evoke two distinct motion percepts (either horizontal or vertical motion percept as shown in Figure 1A) despite a constant, albeit ambiguous, visual input. To understand the contribution of eye-specific information to motion perception, we made use of the bistable motion quartet and manipulated how this display is represented in the early visual areas. Specifically, we attempted to bias perceived direction by presenting separate spatial halves of the motion quartet dichoptically. Here, we demonstrate that eye-specific information is processed more efficiently and can bias overall perception.

Methods

Participants

Fifteen, five, and eight healthy adult volunteers with normal or corrected-to-normal vision participated in the main experiment, stereo fusion control experiment, and utrocular discrimination control experiment, respectively. This study was approved by the institutional review board of Duke-NUS Graduate Medical School Singapore. All subjects gave informed consent and were paid $10.

Stimuli and procedure

The stimulus configuration and experimental procedures of the main experiment are shown in Figure 1. Stimuli used were generated with MATLAB using PsychToolbox (Brainard, 1997; Pelli, 1997). Participants rested their chins on a chin rest and viewed the motion quartet through a mirror stereoscope from a distance of 50 cm. Stimuli were presented against a black background on a 22-in. Samsung 2233RZ LCD monitor with a resolution of $1680 \times 1050$ pixels and a refresh rate of 60 Hz. Throughout the experiment, a white frame (subtending $7.2^\circ \times 7.2^\circ$) remained onscreen to facilitate fusion of the two images. Participants were asked to maintain fixation on a grey central fixation cross (subtending $0.3^\circ \times 0.3^\circ$) during each trial. Eye movements were not monitored during the experiment as the mirror stereoscope setup hampered eye tracking.
The motion quartet display consisted of four square dots (size: 0.3° × 0.3°). Perceptually, illusory motion was elicited by cycling through two frames containing pairs of white squares in diagonally opposite corners of an invisible rectangle. Each cycle lasted 500 ms, with each frame flashed for 250 ms. The horizontal distance between the dots was fixed at 2.3°, while the vertical distance was variable. We attempted to bias participants’ perceived motion direction by varying how the motion quartet was presented dichoptically (Figure 1). In the vertical eye-specific bias condition, the top and bottom spatial halves of the quartet were presented dichoptically (Figure 1B). In this condition, each half would give rise to a vertical motion percept when viewed monocularly. Conversely, in the horizontal eye-specific bias condition, the left and right spatial halves of the quartet were presented dichoptically (Figure 1C). Similarly, in this condition, each half would generate a horizontal motion percept when viewed on its own. The halves were randomly assigned to each eye and counterbalanced.

It is known that the aspect ratio that leads to equal proportion of horizontal and vertical motion percepts (i.e., parity ratio) vary widely amongst individuals (Genç, Bergmann, Singer, & Kohler, 2011; Kohler, Haddad, Singer, & Muckli, 2008). In our experiment, aspect ratios of the presented motion quartets were expressed as the ratio between horizontal over vertical distances. In order to quantify participants’ parity ratio when viewing the motion quartet, we adopted the “Method of Limits” and “Method of Constant Stimuli” procedures described previously (Genç et al., 2011; Kohler et al., 2008). Briefly, the Method of Limits procedure was first employed to estimate each participant’s parity ratio for our main experiment. Subsequently in our main experiment, the Method of Constant Stimuli procedure was used to accurately determine participants’ parity ratio.

Parity ratio estimation

During the experiment, the motion quartet was presented either in the horizontal bias or vertical bias condition. In addition, vertical distance of the quartet was either ramped up (ascending condition) or ramped down (descending condition), thereby altering the aspect ratio of the motion quartet presented. This ramping of vertical distance occurred at a rate of 0.1° every 500 ms for a maximum of 10 s (20 cycles). In perceiving ambiguous motion, the final percept can be influenced by observers’ intention (Kohler et al., 2008; Ramachandran & Anstis, 1985). Thus, participants were tasked to view the display without paying special attention to either motion direction and indicate via button press when their percept flipped from one motion direction to the next.

At the start of the experiment, initial vertical distance of 1.0° was made to be smaller than the horizontal distance. Most individuals have a bias towards perceiving vertical motion when viewing the motion quartet (Genç et al., 2011). Thus, a large initial vertical distance of 6.2° was used for the descending condition to overcome the bias. The large initial distance ensures that all participants perceived horizontal motion when the trial started. Initial vertical distance of the display was made to adapt to each participant’s performance such that perceptual reversals may occur between 5 and 8 seconds after stimulus onset. This adaptation ensures that initial aspect ratio of the motion quartet is sufficiently distinct from the perceptual reversal point, allowing for a clear motion direction percept to arise at the start of each trial. This range also ensured that the initial parity ratio estimation experiment could be completed quickly and efficiently. This adaptation was achieved by increasing or decreasing the initial vertical distance for subsequent trials of the respective condition by 0.1° if perceptual reversals fell out of the 5–8 second range. Order of presentation of trials was randomized and all conditions were counterbalanced. All participants completed 80 trials each. Participants were given between 5–10 practice trials prior to the actual experiment. The parity ratio estimate was computed by averaging aspect ratios of all reversal points across all conditions. Parity ratio estimates ranged from 0.60–1.04.

Main experiment

In the main experiment, participants passively viewed the motion quartets in eight participant-dependent aspect ratios. Horizontal distance of the quartet was kept constant as before, while vertical distance was variable. Parity ratio estimate from the initial experiment was used as one of the eight aspect ratios. Vertical distances of the eight aspect ratios differed from the parity ratio estimate as follows: +1.7°, +1.4°, +0.7°, +0.4°, 0°, −0.4°, −0.7° and −1.4°. The additional +1.7° step was required to overcome the vertical percept bias and ensure good anchor points for the subsequent psychometric fits. The motion quartet was presented either in the horizontal or vertical bias condition for 1.5 s (3 cycles). Participants were then tasked to respond via button press if perceived motion was horizontal or vertical (Figure 1A). All participants completed four blocks of 160 trials each. In each block, order of presentation of trials was randomized and all conditions were counterbalanced. Psychometric fits of behavioral data for each subject was generated using a logistic function on MATLAB.
Stereo fusion control experiment

To ensure that stereo fusion was achieved, subjects were instructed to report immediately when fusion appeared imperfect during the experiment. A separate control experiment was conducted to determine subjects’ ability to detect improper fusion. Five new subjects were recruited for this experiment. Conditions for this experiment were identical to the parity ratio estimation experiment except a second fixation box was presented slightly displaced to the right by 0.2° to mimic improper fusion in half the trials. Participants were tasked to indicate via button press when their percept flipped from one motion direction to another and abort trials where improper fusion was perceived.

Utrocular discrimination control experiment

To ensure that subjects were unaware of the eye of origin of the stimulus, an utrocular discrimination task was performed on eight new subjects. In this experiment, two distinct clusters of small white dots were presented either dichoptically or monocularly for 250 ms. Positions of the clusters were balanced across left and right visual hemifields, and across eyes. Subjects were tasked to compare the dots across the two clusters and indicate if the dots looked similar or different. Each subject completed 240 trials (Figure 2B).

Results

In agreement with previous studies (Gençoğlu et al., 2011; Kohler et al., 2008) participants’ parity ratios varied widely (parity ratio ranges: 0.58–1.40 for horizontal bias and 0.51–0.95 for vertical bias, Figure 4B). A small parity ratio indicates that a rectangle with a large vertical length is required for observers to see equal proportions of horizontal and vertical motion. In the initial parity ratio estimation, no difference in parity ratios was found between vertical bias (mean parity ratio = 0.81) and horizontal bias (mean parity ratio = 0.80) condition, t(14) = −0.27, p = 0.794 (Figure 3). This lack of significant difference could be due to the small number of trials. Nevertheless, eye-specific biases in observers’ motion percept were revealed in their psychometric functions obtained from the main experiment. Psychometric fits of the behavioral data were determined for each subject and depicted in Figure 4A. Mean parity ratio across subjects was significantly smaller in the vertical bias (mean parity ratio = 0.74) condition compared to the horizontal bias.
In the stereo fusion control experiment, all subjects were able to correctly identify improperly fused frames with 100% accuracy in the control trials. Importantly, no subjects reported any improper fusion in the remaining trials. In addition, in the utrocular discrimination control task, no difference was found between the monocular and dichoptic trials, $t(14) = 1.17, p = 0.26$.

**Discussion**

In this study, we have successfully biased participants’ perceived direction of the motion quartet by manipulating the eye-of-origin of separate spatial halves of each motion quartet. This finding suggests a monocular over dichoptic advantage in the perception of apparent motion. This result is consistent with previous binocular rivalry studies where it has been demonstrated that eye-of-origin information contributes to overall percept (Blake, 2001; Hsieh, Colas, & Kanwisher, 2012; Ooi & He, 1999; Shimojo & Nakayama, 1990). In the processing of motion signals, behavioral studies have demonstrated that both monocular and binocular motion components are present. In addition, the proportion of monocular and binocular motion processing varies in different cortical regions (McColl & Mitchell, 1998; Raymond, 1993; Wade, Swanston, & De Weert, 1993). This variation is evidenced by different degrees of interocular transfer of motion aftereffects depending on stimulus parameters.
perceived in the other eye, and therefore interfere with apparent motion perception.

In a similar experiment by Shipley and colleagues (1945), it was determined that under the right conditions, dichoptic is not significantly different from monocular stimulation when perceiving apparent motion (Shipley, Kenney, & King, 1945). This null finding is contrary to what we have demonstrated in our experiment. We suspect that Shipley and colleagues (1945) did not find a difference between monocular and dichoptic stimulation because each subject in their study completed only eight trials, which is significantly fewer in contrast to ours (a total of 8 × 40 trials for each eye bias condition). It is therefore possible that the earlier study lacked statistical power to tease apart differences in monocular versus dichoptic presentation of apparent motion. The difference in findings could also be attributed to differences in experimental paradigms employed: In our experiment, monocular and dichoptic apparent motion were presented simultaneously whilst Shipley and colleagues (1945) chose to present monocular and dichoptic stimuli separately.

By manipulating the direction of apparent motion presented to each eye and measuring proportion of each perceived motion direction, we were able to quantify the effect exerted by each monocular channel on the final motion percept. A unique feature of our motion quartet display is that both monocular and dichoptic apparent motion were made to compete directly with each other for perceptual awareness. The final perceived motion direction would directly indicate the relative strength of monocular versus dichoptic apparent motion presentation. In the experiment described here, we have effectively shown the advantage of monocular over dichoptic stimulation in viewing apparent motion.

**Keywords:** bistable motion, apparent motion, eye-specific information

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**Acknowledgments**

This research was supported by Duke-NUS and National Medical Research Council Cooperative Basic Research Grant (New Investigators Grant) BNIG11nov021 to Po-Jang Hsieh.

Commercial relationships: none.

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References


