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Interocular motion combination for dichoptic moving stimuli

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Abstract—When gratings moving in different directions are presented separately to the two eyes, we typically perceive periods of the combination of motion in the two eyes as well as periods of one or the other monocular motions. To investigate whether such interocular motion combination is determined by the intersection-of-constraints (IOC) or vector average mechanism, we recorded both optokinetic nystagmus eye movements (OKN) and perception during dichoptic presentation of moving gratings and random-dot patterns with various differences of interocular motion direction. For moving gratings, OKN alternately tracks not only the direction of the two monocular motions but also the direction of their combined motion. The OKN in the combined motion direction is highly correlated with the perceived direction of combined motion; its velocity complies with the IOC rule rather than the vector average of the dichoptic motion stimuli. For moving random-dot patterns, both OKN and perceived motion alternate only between the directions of the two monocular motions. These results suggest that interocular motion combination in dichoptic gratings is determined by the IOC and depends on their form.

Keywords: Motion combination; optokinetic nystagmus (OKN); motion perception; intersection-of-constraints (IOC); form.

1. INTRODUCTION

When images moving in opposite directions are presented separately to the two eyes, an alternation in the perception of motion direction occurs (Fox *et al.*, 1975; Blake *et al.*, 1985; Ramachandran, 1991; Wei and Sun, 1992, 1998). If gratings moving in different directions are dichoptically presented, for instance

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with right-tilted grating moving upward to the left to one eye and left-tilted grating moving upward to the right to the other eye, one typically perceives periods of the combination of motion in the two eyes as well as periods of one or the other monocular motions (Banton *et al.*, 1994; Andrews and Blakemore, 1999; Cobo-Lewis *et al.*, 2000; Saint-Amour *et al.*, 2000). Then a question arises: what mechanism is involved in processing such interocular motion combination?

If two gratings moving in different directions are superimposed, the resulting plaid pattern moves with a direction and speed that can be predicted from the intersection-of-constraints (IOC) rule (Fig. 1) (Adelson and Movshon, 1982; Welch, 1989; Simpson and Swanston, 1991). Conversely, in dichoptic stimulation, the individual gratings are incompatible and are not usually combined into a unitary plaid pattern. It has been shown that the perceived direction of combined motion for dichoptic gratings is similar to that predicted by the IOC or vector average rule (Cobo-Lewis *et al.*, 2000). However, it was unknown which rule might underlie the perception of motion combination in that experiment because the IOC and the vector average rules made identical predictions on the direction of combined motion. The vector average rule has been generally applied to predict only the direction of motion combination of plaid (Yo and Wilson, 1992; Cropper *et al.*, 1994), but it could predict both speed and direction of combined motion in locally-paired dot patterns (Curran and Braddick, 2000). Moreover, both direction and speed of motion could be predicted to range from IOC to vector average depending on the stimulus conditions in a Bayesian model (Weiss and Adelson, 1998). These studies of motion combination in vision have been performed mostly under unitary visual field condition. In this paper, we were interested in whether motion combination under dichoptic condition complies with the IOC rule or the vector average rule.

According to the rule of IOC, the velocity of combined motion increases as the direction difference between the two motion signals increases. Whereas, according to the rule of vector average, the velocity of combined motion decreases. By examining the changes of the velocity of combined motion, the rule underlying motion combination would be determined. Usually, psychophysical methods of motion comparison have been used to make quantitative speed judgements (Cavanagh *et al.*, 1984; Hawken *et al.*, 1994; Curran and Braddick, 2000). However, it is difficult to judge the velocity of combined motion during dichoptic stimulation with those methods. Optokinetic nystagmus (OKN), on the other hand, has been suggested to be an objective indicator of the perceived motion for dichoptic gratings moving in opposite directions (Fox *et al.*, 1975). Moreover, for moderate stimulus velocities, the velocity of OKN slow phase is proportional to the stimulus velocity (Collewijn, 1981). Therefore, in the present experiments, we measured OKN eye movements to estimate the velocity of combined motion for dichoptic moving gratings. Our results clearly demonstrate that the velocity of combined motion complies with the IOC rule rather than the vector average rule.

The IOC rule is a geometric construction of two moving gratings, and grating patterns possess both motion and form information. Therefore, interocular motion

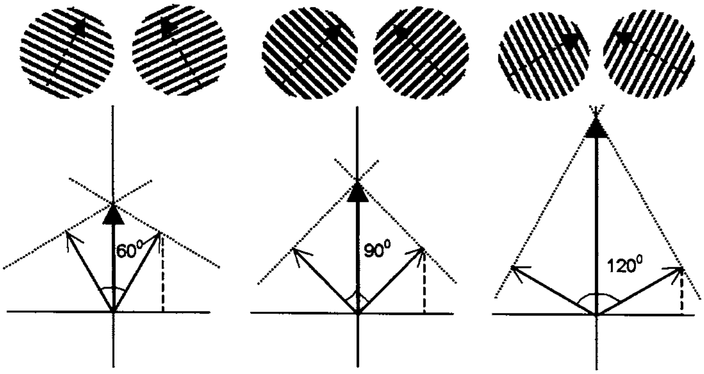


Figure 1. Schematic diagram for the intersection-of-constraints (IOC) of two moving gratings. The interocular direction differences are 60°, 90° and 120°, respectively. The upper panel shows moving patterns and the bottom panel shows the velocity vector determined by the IOC rule. In each direction difference condition, the thin arrows represent the velocities of two motion stimuli, whereas the bold arrows represent the velocity of combined motion predicted by the IOC.

combination might be related to the form information possessed by the moving gratings. To confirm this presumption, we also investigated whether motion combination occurs in dichoptic moving random-dot patterns that lack global form information.

2. GENERAL METHODS

The stimuli were generated by two synchronized computers and presented on two monitors. Two circular visual fields, each subtending 18 deg of visual angle at a viewing distance of 57 cm, were presented separately, one to each eye. A mirror stereoscope enabled each eye to view a separate stimulus. The display itself provided the only source of illumination in the room.

Horizontal and vertical eye movements were measured with the magnetic scleral search coil technique (Robinson, 1963; Wei and Sun, 1998). An annular suction contact lens containing a coil of wire (Skalar Medical BV, Netherlands) was affixed to the subject's right eye. The subject's head was stabilized using a chin and forehead support. Each trial was preceded by calibration measurements in which the subject was instructed to fixate four points sequentially.

Three subjects, all having normal or corrected-to-normal acuity and good stereopsis, participated in the experiment (age range 24–28 years). Two of them were naive with regard to the purpose of study. The study was approved by the institutional human subjects review board, and informed consent was obtained from all subjects.

3. EXPERIMENT 1

3.1. Methods

A square-wave grating of 0.5 cycle/deg was presented within each circular field, with a mean luminance of 4.8 cd/m^2, and a contrast of 95%. For each screen, the grating was orientated symmetrically to the left and right of vertical for the two eyes' views (Fig. 1, top); the angle of orientation to the vertical was 60°, 45° or 30°. Each grating moved in the direction orthogonal to its orientation at a speed of 6 deg/s. Accordingly, the angular difference in direction of motion was 60°, 90° and 120°; the velocity of combined motion predicted by the IOC rule should be 6.9, 8.5 and 12 deg/s upward, or by the vector average rule should be 5.2, 4.2 and 3 deg/s upward.

Each subject was instructed to stare at the stimulus and not to track any specific details. While observing the dichoptic stimulation, the subject reported the perception of upward motion by pressing a key appropriately. Ten trials, each 30 s long, were run for every direction difference. The order of the presentation of the three direction differences was randomly determined. Eye movement signals and the key responses were recorded with a frequency of 100 Hz and stored for off-line analysis.

Eye movement signals were first differentiated to detect their direction and speed by a computer program (with both direction sign threshold and speed threshold). To avoid occasional errors from noise, the OKN direction transition boundaries were checked by visual inspection of OKN eye movements and their derivative traces. The data analysis was performed by a person who had no access to the experiments. For each stimulus condition, the total cumulative time while OKN tracked in a certain direction was divided by the stimulation duration to give the percentage time for each directional OKN. The cross-correlation of direction between upward OKN and upward motion perception, and the slow-phase velocities of upward OKN were also computed.

A control experiment was run to test the velocity relationships between the upward optokinetic response and upward moving stimulus. The stimuli consisted of two identical horizontal gratings presented separately to each eye. Stimulus velocities of 6.9, 8.5 and 12 deg/s were the same for each eye.

3.2. Results

To illustrate the general trend of our findings, a sample of recording is shown in Fig. 2. The upper and middle traces show horizontal and vertical components of the OKN response to dichoptic moving gratings with 120° direction difference. The bottom trace shows the perception of upward motion direction. The eye movement traces clearly illustrated that OKN alternately tracks not only the direction of upward to the left (UL) and upward to the right (UR), but also their combined direction of pure upward (UP). The percentage time for the OKN in three different directions (UL, UR and UP) is plotted at each interocular direction difference in

Fig. 3. Data were averaged across the subjects, as the three subjects showed similar results. The percentage of UP OKN decreases with increasing direction difference. There was no significant directional preference between the UL and UR for the averaged data.

The close match between the UP OKN and the upward motion perception is also readily apparent from inspection of the records. The cross-correlation between eye movement and voluntary report was analyzed in Table 1. The

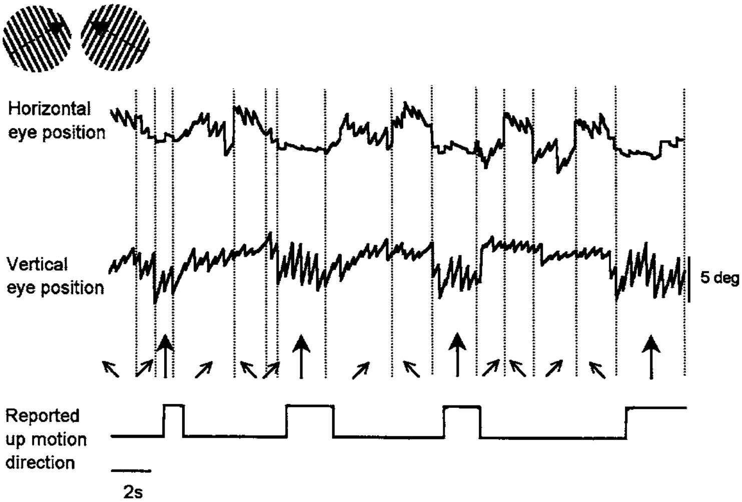


Figure 2. Sample recording of OKN eye movements and the upward motion perception reported for dichoptic moving gratings. The interocular direction difference is 120°; the thin arrows represent diagonal OKN in the direction of each moving stimulus; the bold arrows represent upward OKN in the combined direction.

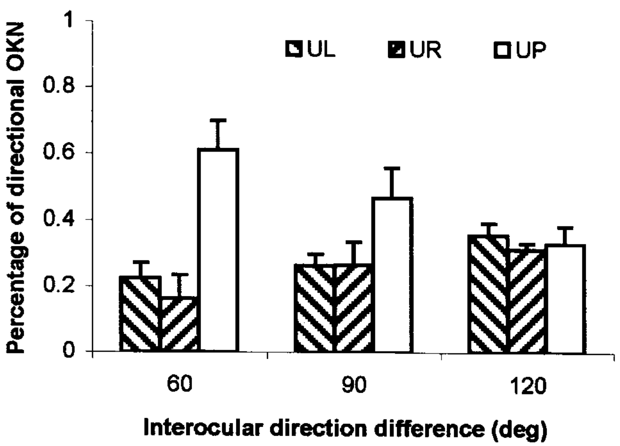


Figure 3. The mean percentage of directional OKN versus the direction difference between the two moving gratings. UL, UR and UP for OKN in the direction of upward to the left (left-tilted bars), upward to the right (right-tilted bars) and pure upward (blank bars), respectively. Error bars for 1 SD.

Table 1.
Cross-correlation of direction between upward OKN and upward motion perception

Subject	Correlation Mean (SD)		
	60 deg	90 deg	120 deg
JLT	0.93 (0.03)	0.94 (0.03)	0.93 (0.03)
RRF	0.87 (0.05)	0.86 (0.05)	0.94 (0.05)
ZHL	0.86 (0.05)	0.86 (0.05)	0.87 (0.07)

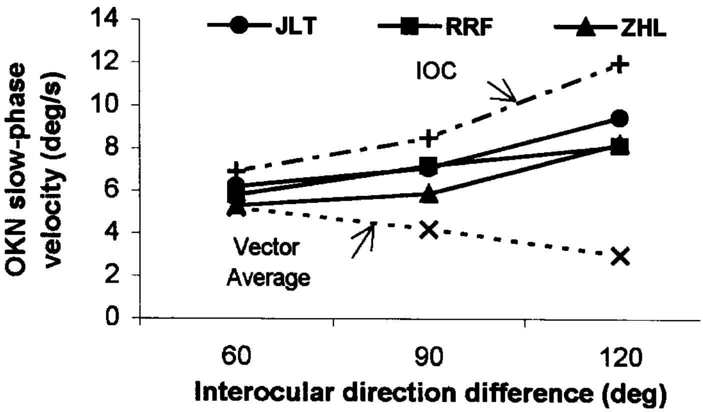
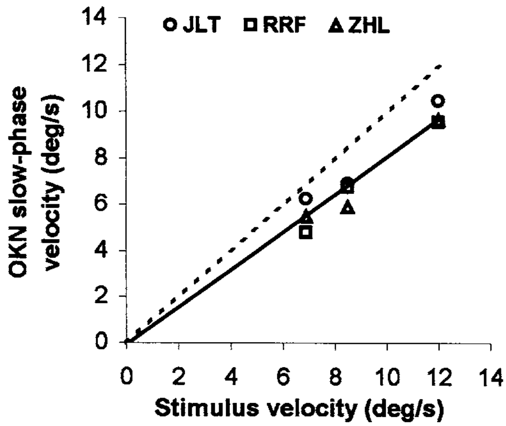


Figure 4. Slow-phase velocity of upward OKN versus the direction difference between the two moving gratings. The results for each subject as indicated; all data showed the velocity of OKN slow phase is not close to the vector average, but close to the IOC.

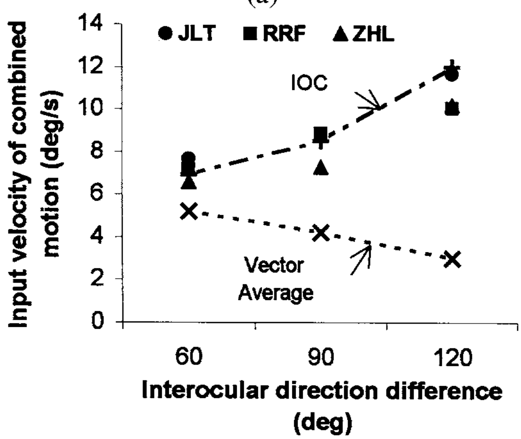
high correlations suggest that the direction of OKN during interocular motion combination correspond to the perceived motion direction.

In Fig. 4, slow-phase velocity of UP OKN is plotted as a function of the interocular direction difference. The dashed line and the dashed-dot line depict the velocities of the vector average and IOC, respectively. The data for all subjects show that slow-phase velocity for the three direction differences tested does not decrease with increasing interocular direction differences, rather it increases with direction differences. It suggests that the combined motion for dichoptic moving gratings is determined not by the vector average of the two motion signals, but rather by the IOC rule.

Considering that the velocity of vertical OKN response is obviously lower than the stimulus velocity (Collewijn, 1981), the velocity of UP OKN to combined motion was further calibrated with that of conventional OKN in the control experiment. The OKN velocities for different upward stimulus velocities are shown in Fig. 5a. The regression line from the data of the three subjects represents the relationships between the optokinetic response and stimulus. Thus, the equivalent input velocity for the UP OKN of combined motion in Fig. 4 is re-plotted in Fig. 5b, which



(a)



(b)

Figure 5. (a) The relationships between the slow-phase velocity of upward OKN response and upward stimulus for three subjects. The dashed line is drawn to show when the OKN velocity equals the stimulus velocity. The data points under this line indicate that the OKN velocity is lower than the stimulus velocity. The straight line represents the regression of the data of three subjects. (b) The equivalent input velocity for upward OKN (re-calibrated data from Fig. 4) versus the direction difference between the two moving gratings.

explicitly shows that the velocity of combined motion for dichoptic moving gratings complies with the IOC rule.

4. EXPERIMENT 2

4.1. Methods

The stimuli consisted of two random-dot patterns (individual dot size 0.08 deg; dot density 50%). Luminance of the dots was 9.7 cd/m^2 and background luminance was 0.01 cd/m^2. For each screen, all dots moved at a speed of 6 deg/s; the two disparate directions of motion were centered around the upward direction and the angular difference in direction of motion was 60°, 90° and 120°. All other parameters of the stimuli and the experimental procedure were similar to those in Experiment 1.

4.2. Results

For dichoptic random-dot patterns moving in different directions, both OKN and perceived motion alternate only between the directions of the two monocular

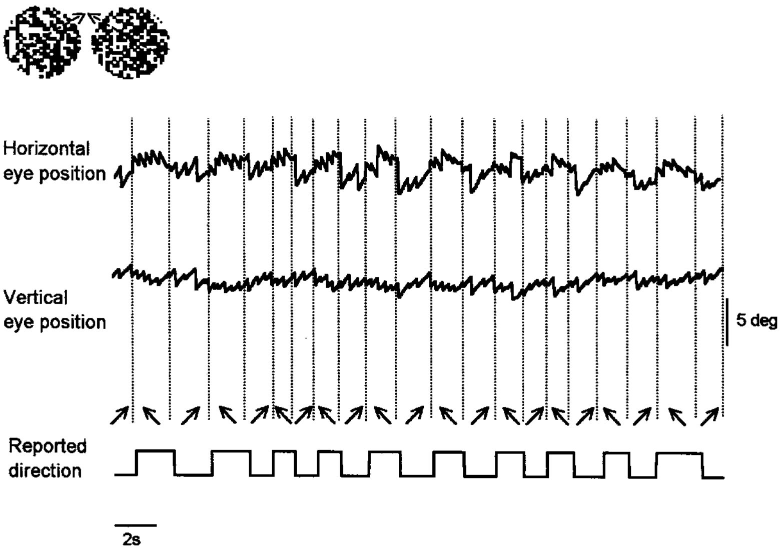


Figure 6. Sample recording of OKN eye movements and the motion perception reported for dichoptic moving random-dot patterns. The direction difference is 120°; all labels are same as in Fig. 2.

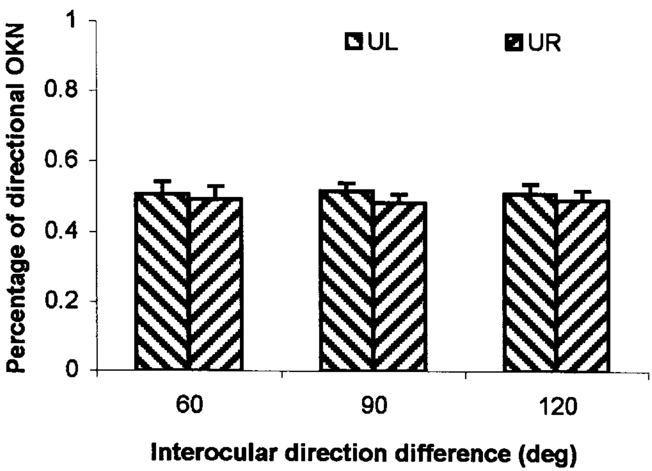


Figure 7. The mean percentage of directional OKN versus the direction difference between the two moving random-dot patterns. All labels are same as in Fig. 3.

motions and do not show the occurrence of upward motion. A sample of these recordings is shown in Fig. 6. The upper and middle traces show horizontal and vertical components of alternating OKN in response to the moving random-dot patterns with 120° direction difference. The bottom trace shows the perceived motion direction. It is clearly illustrated that only diagonal OKN in the direction of each moving stimulus alternates. The percentage time for the OKN in the two directions (UL and UR) is plotted at each interocular direction difference in Fig. 7. There was no significant directional preference between the UL and UR for the averaged data.

5. DISCUSSION

When the two eyes are exposed to dichoptic gratings moving in different directions, OKN alternately tracks not only the direction of the two monocular motions but also the direction of their combined motion. This is consistent with the previous results (Sun *et al.*, 2002). Our results also showed that the OKN in the direction of combined motion is highly correlated with the perceived direction of combined motion. Therefore, OKN eye movement can be used as an objective indicator of motion combination. More importantly, we measured the velocity of combined motion by examining the OKN slow-phase velocity, and the results indicated that the velocity of combined motion in dichoptic gratings complies with the IOC rule rather than the vector average of two monocular motions.

In a recent investigation, the perceived direction for dichoptic moving gratings has been studied (Cobo-Lewis *et al.*, 2000); however, the mechanism responsible for motion combination needed to be determined by further study. In the present experiments, we first quantified the velocity of combined motion and found that the IOC mechanism is underlying the combination of motion across the eyes. According to a previous graphics study, the IOC rule is a simple geometric rule (Fennema and Thompson, 1979). Therefore, we used random-dot patterns to verify whether interocular motion combination occurs in moving stimuli without global form information. Our results showed that such stimuli can yield neither the motion perception in the direction of combined motion nor the corresponding OKN. Consistent results under similar conditions were once reported in a previous study of moving random dots (Blake *et al.*, 1985). The prevalence of motion combination in dichoptic moving gratings but not in random-dot patterns suggests that motion combination in dichoptic moving stimuli depends on their form.

This association of form information with motion combination seems incompatible with the finding which suggests that interocular combined motion and form are independent (Andrews and Blakemore, 1999). This discrepancy was probably due to the distinct stimulus design (Cobo-Lewis *et al.*, 2000). For instance, short durations (1.5 s) were used in their experiment, whereas we used prolonged presentation (30 s), which ensured the natural occurrence of motion combination. In addition, our stimuli were much larger (18 deg) than theirs (0.8 deg) because large stimulus fields are necessary to elicit distinct OKN and to facilitate the global motion perception. Although the large stimuli would yield piecemeal rivalry (Blake *et al.*, 1992), it is well established that motion enhances predominance during binocular rivalry and the incidence of piecemeal rivalry decreases with the velocity of motion (Blake *et al.*, 1985). Therefore, our dichoptic stimuli (the gratings moving at a relatively high velocity of 6 deg/s) scarcely evoked piecemeal rivalry. Instead, most of the subjects reported that V-shaped or inverted V-shaped patterns were seen when the combined motion was perceived. Such pattern might result from the interocular grouping of two gratings arriving from different eyes (Kovács *et al.*, 1996). Yet with random-dot patterns, no such interocular grouping is possible due to the lack of corresponding form information.

Our results that motion combination occurs in gratings but not in random-dot patterns under dichoptic condition seemed similar to those under traditional monoptic and dioptic conditions (Marshak and Sekuler, 1979; Adelson and Movshon, 1982; Welch, 1989; Lorenceau, 1996). Additionally, our result showed that the percentage time of OKN to combined motion depends on the direction difference between the two monocular motions, which was also similar to the result of plaid (Cao and Sun, 1997). Although these findings suggest that motion combination of dichoptic gratings and plaid might be governed by similar rules, the IOC rule in plaid is possibly induced by the intersections of the moving plaid (Adelson and Movshon, 1982; Welch, 1989; Alais *et al.*, 1996). Instead, with dichoptic presentation of moving gratings, there is no such physical intersection in the input of the retinal image. Conforming to the IOC rule in dichoptic gratings, there must be an interocular grouping, or reassembling, of portions of the two physical stimuli to provide the percept of the latent ‘intersection’. This interocular grouping not only shows the association with geometric form information, but also suggests that higher cortical areas may be involved in processing the combined motion.

Such interocular motion combination should arise at or beyond the convergence of two monocular signals. However, one question that remains unanswered is the neural locus of motion combination. Previous physiological work found that a subset of MT neurons (about 25%) are selective for pattern motion (Movshon *et al.*, 1985; Rodman and Albright, 1989). These pattern selective neurons in area MT may solve motion combination by neurally implementing the IOC rule. However, in dichoptic moving gratings, different from the plaid patterns, each eye views a grating separately and neither eye has access to the entire plaid. Therefore, such a supposition needs further electrophysiological testing to determine the precise neural locus involved in the process of interocular pattern motion.

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