Two-Dimensional Optokinetic Nystagmus Induced by Moving Plaids and Texture Boundaries

Evidence for Multiple Visual Pathways

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Horizontal and vertical components of optokinetic nystagmus (OKN) were measured using the magnetic search coil technique in normal human adults during presentation of simple and complex moving patterns. Simple patterns were gratings moving horizontally and obliquely. Complex moving patterns consisted of plaids formed by superimposed oblique motion of two sets of gratings or of illusory contours formed by offset discontinuities in gratings. Slow-phase OKN gains (eye velocity divided by stimulus velocity) induced by high-contrast type I and type II plaids were comparable with those generated by one-dimensional moving gratings. The axis of OKN for high-contrast plaids was along the resultant direction determined by the intersection-of-constraints rule and not along any component. With low-contrast presentations, OKN induced by type I patterns remained in the resultant direction, but the OKN direction induced by type II patterns was biased toward the components’ directions. The OKN generated by texture boundaries embedded in real pattern motion was measured for motion of illusory contours having systematically varying directions. The gain of OKN induced by real motion was independent of the direction of illusory contour motion, but the gain to illusory contour motion decreased with increasing contour angles. All these results suggest that input signals for driving the optokinetic system come from visual areas extracting higher order two-dimensional motion information.

Visual tracking serves to stabilize the images on the retina of moving objects. Tracking is believed to be mediated by both the smooth pursuit system and the optokinetic system. The smooth pursuit system allows tracking of a small target by the fovea; the optokinetic system responds to a large field stimulus. Neuroanatomic areas involved in generating smooth pursuit include the retinogeniculate-occipital pathway, parietal cortex, cerebellum, and parts of the brainstem.1 Two pathways have been identified in the generation of the slow phase of optokinetic nystagmus (OKN).2 The “subcortical” or “slow” pathway is dominant in afoveate animals and leads to slow buildup of OKN.3,4 This pathway also is called the “indirect” pathway, acting through the velocity storage mechanism, which is also responsible for mediating optokinetic after nystagmus (OKAN). The second tracking pathway is the “cortical” or “fast” pathway, mediating the rapid onset of OKN. This pathway, is dominant only in primates, also is called the “direct” pathway, and is probably not associated with OKAN.3,4 Even though the subcortical pathway is phylogenetically older than the cortical pathway, in adult humans, the cortical pathway is so dominant that OKN can be elicited rarely after cortical lesions.4

Relatively little is known about the visual information that the cortical pathway conveys, or where the visual information is relayed. In the cat, binocular and directionally tuned neurons in areas 17 and 18 contribute to the cortical pathway.5 The distinction between optokinetic and smooth pursuit systems in mediating eye movements in humans has been ambiguous, however, in ocular motor physiology. The cortical pathway for OKN is dominant in foveate animals, and flocculectomy disrupts both the fast OKN system and the smooth pursuit system.6 However, even in

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humans, because sustained unidirectional stimulation of a large portion of the visual field elicits the alternating pattern of slow and quick phases typical of "nystagmus," for the sake of simplicity, we will call this response OKN (Fig. 1).

Classically, OKN has been tested in humans using stimuli consisting of stripes moving in a single direction. Based on the known motion pathways in the human visual system, we employed the special properties of two-dimensional patterns to explore the characteristics of inputs evoking OKN. A two-dimensional pattern consists of light intensity changes in both the horizontal and the vertical axes; a one-dimensional image, like a stripe or a grating, consists of intensity change only along one axis (Fig. 1, top left). Two-dimensional moving plaid patterns were created by superimposing two one-dimensional moving gratings of different orientations. The right side panels in Figure 1 show the velocity space construction for calculating the resultant motion. This intersection-of-constraints rule (IOC) rule for determining resultant speed and direction is different from a vector sum or vector average. Any pair of vectors that emanate from the origin to the circumference of the circle will produce a resultant extending from the origin to the opposite point on the circle. The speed of the resultant is determined by the diameter of the circle. Two-dimensional plaids were classified into two groups: the type I plaid (Fig. 1, middle) consists of one component vector lying on each side of the resultant. The type II plaid (Fig. 1, bottom) consists of two components both lying on the same side of the resultant. The perceived direction of moving type I and type II plaids has been measured psychophysically by others, who proposed that two-dimensional motion processing occurs in two stages. One-dimensional component motion vectors are signaled by the first-stage motion-sensitive detectors. The outputs from these detectors, when matched in a range of spatial frequency, velocity, and contrast, are combined selectively in the second stage to generate the resultant vector. One study found that 40% of cortical area MT neurons in the monkey were only sensitive to component directions when stimulated by moving plaids. Another 25% were found not to respond significantly to the component grating directions when the components were presented alone, but they responded well to (1) the resultant direction when both components were presented simultaneously and (2) a one-dimensional grating traveling in the plaid resultant direction. These investigators suggested that the pattern selective neurons in MT receive input from component direction selective neurons in V1 and MT and solve for the resultant two-dimensional pattern direction by neurally implementing the IOC rule. Others proposed that this could be accomplished by negative feedback among MT neurons. In their model, a pattern unit exerts strong recurrent inhibition on units tuned to directions ±45°, ±60°, and ±75° away from its preferred direction. Therefore, units responding to the plaid resultant direction would inhibit those responding to the plaid components, and the overall output from MT would only signal the resultant motion of the plaid.

The first kind of two-dimensional image used in these experiments was a type I plaid pattern with a horizontal resultant motion. It was created by superimposing two sinusoidal gratings directed 45° above and below the horizontal meridian. The question considered was whether the optokinetic system responds to the component vectors or to the overall pattern resultant vector. If the optokinetic system exclusively receives input from MT, then component motions may be invisible, and OKN would be in the direction of the resultant. However, if the optokinetic system receives substantial input from component selective neurons in the brainstem or lower visual areas, then direction asymmetries in motion sensitivity may sum vectorially to produce an OKN direction biased toward a component and away from the resultant. Gains of vertical OKN have been reported to be greater for upwardly directed stimulus motion than for downward motion. The gains of vertical OKN also were found to be greater for upward stimulus motion than for downward motion. Therefore, if the second hypothesis were correct, the OKN axis induced by a horizontally moving plaid pattern would deviate upward from the horizontal. Alternatively, if the first hypothesis were correct, then even large asymmetries in vertical OKN gain would not affect the tracking of the horizontally moving resultant.

It was hypothesized that the IOC rule applies to determining resultant motion for both type I and type II plaids, but perceptual differences have been characterized by others. It was found that, with short-presentation durations (<60 msec) or with low-contrast presentations, perceived direction of type II plaid motion is biased toward the components. Type I motion perception, however, is independent of presentation duration and contrast, suggesting the neural mechanisms underlying type I and type II motion processing to be distinct. Accordingly, the second kind of two-dimensional images used in these experiments consisted of type II plaids (Fig. 1, bottom). We examined the effect of contrast for both type I and type II plaids (Fig. 2).

The third kind of two-dimensional images used in
Fig. 1. Stimulus patterns constructed with sinusoidal gratings. Left sides show images and right sides show velocity space constructions of the motion vectors. (Top) One-dimensional sinusoid moving in the +45° direction (counterclockwise to horizontal axis). When a grating in the +45° direction (C1) is superimposed with one moving in the -45° direction (C2), a type I plaid is produced (Middle). (Bottom) Type II plaid in which both components lie on the same side of the resultant. Note that the intersection of constraints (IOC) resulting from a type I pattern lies between the component vectors, whereas the IOC resulting from a type II pattern does not.
these experiments consisted of vertically oriented square wave gratings moving downward. A portion of the light and dark borders was shifted horizontally and vertically to create illusory contours (Fig. 2). As these illusory contours were built up by alternating light and dark stripes, the average light intensity across them equaled the mean luminance. Therefore, the motion of illusory contours should be invisible to directionally tuned neurons in cortical area V1, and the detection of illusory contours would require higher level visual processing. Two major motion pathways have been found to project in parallel from V1 to MT in primates. The direct pathway arises from layer 4b in V1; the indirect pathway reaches MT through V2. It was found that 44% of V2 neurons respond to pattern discontinuities or subjective contours. Based on the finding that the pursuit system receives input from MT and that the pursuit system is related to the optokinetic system in primates, it was predicted that OKN would be elicited by the motion of texture boundaries.

Materials and Methods

Spatial patterns were generated on a Macintosh (Cupertino, CA) IICX microcomputer interfaced to a Covid video distribution adapter and back projected by a Sony Multiscan video projector onto a translucent tangent screen placed 56 cm from the subject's eyes. The images were displayed in a circular field with a diameter of 90° in a darkened room. The mean image luminance was 13 cd/m². Contrast was defined as \((L_{\text{max}} - L_{\text{mean}}) / L_{\text{mean}}\), where \(L_{\text{max}}\) and \(L_{\text{mean}}\) were maximum and mean luminances in the pattern. Pattern motion was achieved using color table animation (described in detail elsewhere). All directions were defined counterclockwise from the horizontal (Fig. 1).

In the one-dimensional grating experiment, the spatial frequency of the sinusoidal grating was 0.088 cpd, and the contrast was 0.52. The horizontal speeds were 34 and 68°/sec. The speed tested in diagonal directions (± 45°) was 34°/sec. In the type I plaid experiment, motion pattern was created by superimposing two perpendicularly oriented 0.088 cpd sinusoidal gratings. The components moved diagonally with equal speeds of either 22.7 or 45.4°/sec, producing horizontal resultant speeds of 32 or 64°/sec. In the type II plaid experiment, pattern motion was created by superimposing two 0.088 cpd sinusoidal patterns oriented at 19.5° and 41.8°. Component C1 moved at 12.5°/sec, and component C2 moved at 25°/sec. The resultant was 37.5°/sec directed horizontally. For high-contrast presentations, the contrast of each component was 0.26, and the overall pattern contrast was 0.52. For low-contrast presentations, overall pattern contrast was reduced to 0.08. Stimulus presentations were interleaved randomly, lasted 10 sec, and were presented twice for each direction. The patterns randomly drifted to the left or right to avoid motion adaptation and anticipatory eye movements. Instead of replicating all subjects using all parameter variations, the type I plaid speed was varied for three subjects, and pattern contrast was varied in the other three. This was done to prevent prolonging the experiments to more than 30 min in duration.

Illusory contours of various orientations were created by offsets at various angles in vertically oriented square wave gratings moving downward. A portion of the light and dark borders was shifted horizontally and vertically to create illusory contours (Fig. 2). As these illusory contours were built up by alternating light and dark stripes, the average light intensity across them equaled the mean luminance. Therefore, the motion of illusory contours should be invisible to directionally tuned neurons in cortical area V1, and the detection of illusory contours would require higher level visual processing. Two major motion pathways have been found to project in parallel from V1 to MT in primates. The direct pathway arises from layer 4b in V1; the indirect pathway reaches MT through V2. It was found that 44% of V2 neurons respond to pattern discontinuities or subjective contours. Based on the finding that the pursuit system receives input from MT and that the pursuit system is related to the optokinetic system in primates, it was predicted that OKN would be elicited by the motion of texture boundaries.
alternating light and dark stripes. Each stripe was 1.35° wide and 28° high. The stripes moved vertically downward at a speed of 54°/sec. Each experiment contained duplicate presentations of randomly interleaved illusory contours at -63.4°, -45°, -26.6°, 0°, 26.6°, 45°, and 63.4° from the horizontal axis. Illusory motion vectors induced by these contour angles would be at corresponding angles from the vertical axis (Fig. 2). Contrast was fixed at 0.55. The presentation duration was 10 sec.

A total of six naive paid normal adult volunteers participated in these experiments. They gave written informed consent according to the protocol approved by the Institutional Review Board after procedures were explained to them in detail. We measured OKN during binocular viewing by instructing subjects to track the movement of the patterns without following any individual feature. Gains were computed vectorially from horizontal and vertical components by dividing the mean slow-phase eye velocity by the target velocity. Eye movements were recorded using the magnetic search coil technique. The method is sensitive to eye movements as small as 20 min of arc with a range of 30°.

An annular suction contact lens containing a coil of wire (Skalar Medical, Delst, The Netherlands) was affixed to the subject's right eye after topical anesthesia was administered with proparacaine 0.5%. Each experiment was limited to 30 min; at the end of this time, the contact lens was removed. The subjects' heads were positioned comfortably in a padded restraint to maintain a constant viewing distance. Calibration was obtained by averaging responses to three to five sets of target displacements in the horizontal and vertical directions to 10° eccentricity around the primary position. Horizontal and vertical eye speeds were monitored in real time by analog differentiation of corresponding position signals and were displayed on line using a rectilinear polygraph. Simultaneously, digital data acquisition and storage were done by a second Macintosh II computer equipped for analog-digital conversion at 200 Hz with 12-bit precision using custom software operating under the Lab VIEW package (National Instruments, Austin, TX). After digital differentiation and low-pass filtering, fast components were identified digitally and removed using velocity, acceleration, and duration criteria. Mean OKN velocity was computed automatically off line over a 6-sec interval during stimulus presentation.

### Results

**OKN Induced by Sinusoidal Gratings and Plaids**

We first measured eye movements induced by one-dimensional sinusoidal gratings moving horizontally.

The OKN gains at two different speeds are shown at the top of Figure 3. The average gain for five subjects measured with 34°/sec patterns was 0.57, with a standard error of the mean (SEM) of 0.14. The average gain measured with 68°/sec patterns was 0.38 ± 0.13. These gains were lower than those reported by other investigators using full-field stimulation but were consistent with values obtained by others using stimuli having restricted spatial extent or visible fixed reference contours in the periphery. The bottom of Figure 3 shows OKN gain measured in three subjects with type I plaids whose resultants moved horizontally. The speeds were calculated (using the IOC rule) to be 32 and 64°/sec. The average gain and SEM at 32°/sec was 0.76 ± 0.16; and at 64°/sec, it was 0.63 ± 0.23. A four-way analysis of variance test indicated that gains measured with these two kinds of patterns at these two speeds were not significantly different at the $P = 0.05$ level (Fig. 3).

![Fig. 3. OKN induced by one-dimensional (1-D) sinusoidal gratings and type I plaids at two different stimulus speeds. Means and standard deviations for different subjects ($n = 6$ in Top; $n = 3$ in Bottom) are shown together with the pooled mean and standard error of the mean.](http://iovs.arvojournals.org/pdfaccess.ashx?url=/data/journals/iovs/933394/)
Next, we investigated OKN produced by diagonally moving one-dimensional gratings and plaids presented at different contrasts. The velocity space constructions of these patterns are shown in Figure 1. The diagonally moving gratings had a speed of 34°/sec at 45°, 135°, 225°, and 315°. The pairs of components of the type I plaids drifted at a speed of 22.7°/sec either in the 45° and the 315° directions or in the 135° and the 225° directions, creating resultant vectors moving at 32°/sec in the 0° or 180° directions. Type II plaid motion was produced by combining component vectors at 70.5° (C1) and 48.2° (C2), or at 250.5° (C1) and 228.2° (C2). Component C1 moved at 12.5°/sec, and C2 moved at 25°/sec. The resultant vector moved at 37.5°/sec either in the 0° or the 180° direction.

Two representative subjects’ data are shown in Figure 4. The averaged data from various subjects are shown in Figure 5. These results are displayed in polar form; the direction of eye movement is indicated by the angle, and the gain is indicated by the distance from the center to the point. Overall gains of subject SS are lower than those of subject DH, indicating a range of individual performances. Figure 3 (top) shows that the OKN gain induced by horizontally moving gratings is also larger for subject DH than for subject SS. In general, response directions for diagonally moving patterns varied idiosyncratically in individual subjects, but the mean response direction more closely approximated the stimulus direction (Fig. 4).

Averaged OKN data are shown in Figure 5. The gains for diagonal gratings and high-contrast type I plaids represent averages from six subjects. The gains measured under other conditions represent averages from three subjects. In response to horizontally moving type I plaids of high and low contrast, OKN was purely horizontal, and the gain was independent of contrast. However, OKN induced by type II plaids was influenced by contrast. At low contrast, OKN axis was biased toward the components’ directions. At high contrast, the OKN direction was along the IOC resultant direction.

The OKN gain induced by the four diagonally moving gratings averaged over all directions was 0.60 ± 0.06. For diagonally moving gratings in the 45° and 135° directions, it averaged 0.56 ± 0.09.
and 315° directions, OKN gain averaged 0.63 ± 0.07 (P > 0.05, by two-tailed student t-test). This suggests that pooled average upward OKN gain was equal to the downward gain for these six subjects, even though there are idiosyncratic directional differences in vertical pursuit and OKN gains for individual subjects (data not shown here). The average axis of OKN induced by diagonally moving gratings was 39.7 ± 2.7° rather than being purely diagonal (45°). This suggests that OKN gain is greater in the horizontal than in the vertical direction.

The OKN gains induced by high-contrast type I, low-contrast type I, and high-contrast type II plaids averaged 0.57; they were not significantly different from those induced by diagonally moving gratings (P > 0.05, by two-tailed student t-test). The OKN generated by low-contrast type II patterns had a much smaller gain of 0.3 ± 0.05, significantly smaller (P < 0.05, by two-tailed student t-test) than the gain induced by one-dimensional patterns at a comparable speed. The OKN directions were 0.0 ± 1.34° for high-contrast type I plaids, −0.8 ± 1.9° for low-contrast type I plaids, +6.6 ± 3.0° for high-contrast type II plaids, and +47.3 ± 5.4° for low-contrast type II plaids. Only for low-contrast type II plaids did the direction of tracking differ significantly from the horizontal at P = 0.05 (by the two-tailed student t-test). For high-contrast type I plaids, low-contrast type I plaids, and high-contrast type II plaids, the directions of tracking were not significantly different from the horizontal (P > 0.05, by two-tailed student t-test; Fig. 5).

OKN Induced by Texture Boundaries

A representative stimulus used for this measurement is shown in Figure 2 (upper panel). It consists of a vertically oriented square wave grating with a 180° horizontal phase shift and vertical offset creating an illusory contour moving perpendicular to its orientation. The horizontal component of this vector is generated by the illusory contour; the vertical component of this vector is generated by real motion. Typical analog eye position and velocity data of subject CO are shown in Figure 6. The left panels show OKN in response to an illusory contour oriented at 0°, i.e., moving directly downward (Fig. 2, top). The right panels show OKN in response to an illusory contour oriented at −63.4° traveling obliquely. The vertical contour motion induced only vertical OKN; oblique contour motion induced both horizontal and vertical OKN (Fig. 6).

A total of six subjects participated in this experiment. The OKN velocities induced by real and illusory motion vector components are shown in Figure 7. Data in the panels at left represent OKN induced by real motion as the light and dark borders drifted directly downward at 54°/sec, irrespective of the illusory contour orientations. In response to real component motion, OKN speed and gain are independent of orientation of the illusory contour. The real compo-

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Fig. 6. Analog tracking of eye position and velocity. (Left) OKN in response to an horizontally oriented illusory contour moving directly downward. (Right) OKN in response to an illusory contour oriented at −63.4° travelling obliquely.
nent gain varied idiosyncratically from approximately 0.3 for subject SS to 0.8 for subject DH. These values were similar to the gains induced by the sinusoidal gratings shown in Figure 3 (top). Data on the right of Figure 7 represent OKN induced by illusory contours. Positive speeds indicate OKN to the right. The overall trend was that horizontal speed was greater for illusory contours oriented more vertically. When the illusory contour was in the $-63.4^\circ$ direction, all subjects exhibited leftward OKN slow phases. However, when the illusory contour was in the $+63.4^\circ$ direction, four subjects showed rightward OKN slow phases, and subjects DH and ET still displayed leftward slow phases. Subject CO was the most sensitive to changes in angle of the illusory contour; subjects DH and ET showed little change. Gain was obtained by dividing slow component speed by calculated illusory horizontal contour speed. For orientations at $0^\circ$, $26.6^\circ$, $45^\circ$, and $63.4^\circ$, the corresponding horizontal illusory motion speeds would be 0, 27, 54, and $108^\circ$/sec, respectively. Illusory motion gain is undefined at $0^\circ$ because the illusory motion component in the horizontal direction is zero. In general, illusory motion gain decreased with increasing contour angles, corresponding to increasing illusory motion speeds (Fig. 7). The horizontal OKN gain observed here agrees with the low OKN gain induced by second-order motion stimuli reported by others.39

The direction of OKN induced by texture boundaries is shown in Figure 8. The OKN direction was calculated as the arctangent of the horizontal eye speed divided by the vertical eye speed. The top graph shows each individual subject's data, and the bottom graph shows the pooled data for six subjects. The dotted line shows the ideal direction if the slow components were directed perpendicularly to the illusory contour. The results show that there is a small but persistent bias in OKN toward the illusory contour motion vector (Fig. 8).

Discussion

In these experiments, we used the special properties of two-dimensional patterns to explore underlying inputs driving the optokinetic system. Because the cortical pathway for mediating OKN may be related to smooth pursuit in primates and the distinction between human OKN and smooth pursuit has not been established clearly in ocular motor physiology, in this article, we operationally used the term "OKN" to describe eye tracking movements induced by large field stimulation. The data indicate that OKN gains for one-dimensional sinusoidal gratings and horizontally moving type I plaids are not significantly different. The axis of OKN induced by diagonally moving gratings was restricted toward the horizontal meridian (consistent with the finding that vertical pursuit gain is lower than horizontal pursuit gain).35 We explored the possible asymmetry in upward and downward
The OKN gain and direction for type I plaid was found to be independent of contrast. Alternatively, OKN induced by type II plaid was influenced by contrast. At low contrast, the OKN axis was found to be significantly biased toward the components' directions. This finding agreed with perceptual data reported previously. At high contrast, the OKN direction approximated the resultant direction but with a bias of +6.6 ± 3.0° toward the components. Even though this objectively measured bias was not significantly different from 0° (P > 0.05), the perceived direction of type II patterns at high contrast was found using psychophysical techniques to be biased toward the components by approximately 5°. The OKN gains induced by high-contrast type I, low-contrast type I, and high-contrast type II plaids were not significantly different from those induced by one-dimensional moving gratings. The OKN generated by low-contrast type II patterns had a much smaller gain than that generated by one-dimensional patterns moving at a comparable speed. The vector average calculated from the components of the type II plaid (Fig. 1, bottom) was 60° from the horizontal axis and had a magnitude of one half the IOC resultant speed. Therefore, the components of type II plaids, presented at low contrast, may serve as input signals to the optokinetic system.

Type I motion processing could be approximated crudely by averaging the output from component selective units or doing a vector summation operation. Type II motions offer a more rigorous test of the IOC rule than type I motions because the predicted results differ from the average of the component vectors. The processing of type II motion also presents a greater challenge to the visual system because the direction signals measured at the primary motion detector level are very different from those derived at the

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Fig. 8. OKN direction induced by texture boundaries. Top graph shows each of six individual subject's data, and bottom graph shows the pooled data. Error bars indicate the standard errors of the means. The dotted line shows the ideal direction if the slow components were directed perpendicularly to the illusory contour.

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gains in OKN by calculating the gains of diagonally moving gratings in the 45° and 135° directions compared with those induced by diagonals in the 225° and 315° directions. The upwardly directed diagonals had a gain of 0.56 ± 0.09; the downwardly directed diagonals had a gain of 0.63 ± 0.07. This difference was not statistically significant (P > 0.05, by two-tailed student t-test). This suggests that the average upward OKN gain was equal to downward gain for these six subjects, even though there was idiosyncratic vertical OKN gain asymmetry in individual subjects. Directional asymmetries for vertical OKN have been reported to favor upward motion. If input signals to the optokinetic system arise from units that respond to components moving in the ±45° directions, then asymmetry in vertical optokinetic gain should cause OKN direction for type I plaids to be biased toward the direction with the higher gain. Because observed OKN directions for type I plaids were purely horizontal for all subjects, it appears that the input to the optokinetic system derives from pattern selective rather than from component selective units. This hypothesis could be tested further in patients with large asymmetries in vertical OKN gain. If the sensory input to the optokinetic system really originates in units that determine the plaid resultant direction, then OKN in response to these type I plaids will be purely horizontal. Furthermore, patients with a lesion in the middle temporal cortical area, which houses the putative pattern selective neurons, might manifest oblique OKN directions when stimulated by plaids with horizontal IOC resultants.

The OKN gain and direction for type I plaids were found to be independent of contrast. Alternatively, OKN induced by type II plaids was influenced by contrast. At low contrast, the OKN axis was found to be significantly biased toward the components' directions. This finding agreed with perceptual data reported previously. At high contrast, the OKN direction approximated the resultant direction but with a bias of +6.6 ± 3.0° toward the components. Even though this objectively measured bias was not significantly different from 0° (P > 0.05), the perceived direction of type II patterns at high contrast was found using psychophysical techniques to be biased toward the components by approximately 5°. The OKN gains induced by high-contrast type I, low-contrast type I, and high-contrast type II plaids were not significantly different from those induced by one-dimensional moving gratings. The OKN generated by low-contrast type II patterns had a much smaller gain than that generated by one-dimensional patterns moving at a comparable speed. The vector average calculated from the components of the type II plaid (Fig. 1, bottom) was 60° from the horizontal axis and had a magnitude of one half the IOC resultant speed. Therefore, the components of type II plaids, presented at low contrast, may serve as input signals to the optokinetic system.

Type I motion processing could be approximated crudely by averaging the output from component selective units or doing a vector summation operation. Type II motions offer a more rigorous test of the IOC rule than type I motions because the predicted results differ from the average of the component vectors. The processing of type II motion also presents a greater challenge to the visual system because the direction signals measured at the primary motion detector level are very different from those derived at the
second motion-processing stage. It was hypothesized that, to calculate the type II resultant motion correctly, an extra processing stage must create compensatory signals to defeat the direction bias toward the components elicted by component selective units. At short presentation durations (< 60 msec), compensatory direction signals for type II motion processing are unavailable, thus leading to a direction bias toward the component directions.

End-stopped neurons in area V2 were found to be specialized for the detection of illusory or subjective contours. Type II motion might generate direction signals in cortical area V2 based on the motion of illusory contours extrapolated along the nodes (areas of mean luminance) in the image. In Figure 1 (bottom left), which shows a type II plaid, the motion of illusory contours formed by the nodes would be toward the lower right. The downward bias created by the illusory contour motion signaled by the V1–V2–MT pathway, then would cancel the upward bias created by the components signaled by the V1–MT pathway to create a horizontal perceived direction.

Accurate perception of type II motion involves an additional processing stage (V2), and it was anticipated that type II motion would be degraded more significantly by decreasing the signal-to-noise ratio. When the signal-to-noise ratio of two-dimensional motion was decreased by decreasing the pattern contrast to 8%, type II motions were found to generate large eye movement biases toward the components.

To our knowledge, this is the first report of human OKN generated by texture boundaries measured during motion of illusory contours. The OKN gain induced by real motion was found to be independent of the illusory contour angle, but the OKN gain induced by illusory contour motion decreased with increasing contour angles. This suggests that the motion pathway processing Fourier motion (motion comprised of intensity changes perpendicular to the direction of motion) does not respond to illusory contours. The motion pathway responsible for signaling non-Fourier motion is affected by illusory contours. In the fovea, the perceived direction of motion was nearly perpendicular to the illusory contour orientation; at 16° in the periphery, the perceived direction was much closer to the real direction of motion. For the illusory contour oriented at 45°, the mean bias was approximately 40° when measured in the fovea and 20° when measured in the periphery. Wilson and Mast concluded that (1) both the Fourier and the non-Fourier pathways are operating to analyze motion in the fovea but (2) the human periphery lacks the non-Fourier pathway and is only able to signal the true direction of motion elicited by Fourier components.

It might have been anticipated that the objective OKN axis for illusory contour motion would correspond to psychophysical measurements of perceived direction. However, pooled data indicate that the axis corresponding to maximum illusory OKN only deviated approximately 10° from the real direction of motion. There are two explanations for the weaker effect of illusory contours seen in our OKN data. First, the stimulus diameter was 90°, stimulating a much larger portion of Fourier responsive peripheral retina than in the psychophysical experiments. Second, we found that OKN gain generated by illusory contours declined with increasing illusory contour speed. In our experiment, the patterns moved at 54°/sec; in the earlier study, speeds were less than 10°/sec. With lower illusory component gain, the OKN axis would be less biased toward the illusory motion vector.

Type II plaids have been used to explore the contribution of cortical and subcortical pathways to the optokinetic system. Other investigators have found that the subcortical pathway is more dominant in the cat, but the cortical pathway may play a more significant role in the human. Our results are consistent with the notion that the cortical pathway is dominant in humans because OKN responses were obtained for two-dimensional motion stimuli containing non-Fourier motion information (invisible to the subcortical pathway). A quantitative model of two-dimensional motion processing based on parallel cortical pathways from V1 and V2 to MT was developed to explain the perceptual characteristics of two-dimensional motion. This model contains a motion energy pathway representing V1–MT processing and a texture boundary motion pathway representing V1–V2–MT processing. The OKN data we presented support this concept and suggest that the cortical pathway that evokes OKN in humans also can be subdivided into at least two visual pathways specialized in processing higher order motion information.

Key words: optokinetic nystagmus, two-dimensional motion, intersection-of-constraints, illusory contour motion processing

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