

Brain stem and cortical contributions to the generation of horizontal optokinetic eye movements in humans

LAURENCE R. HARRIS,¹ TERRI L. LEWIS,² AND DAPHNE MAURER²

¹Department of Psychology, York University, Toronto, Ontario

²Department of Psychology, McMaster University, Hamilton, Ontario

(RECEIVED June 2, 1992; ACCEPTED July 29, 1992)

Abstract

We evaluated the subcortical pathways' contribution to human adults' horizontal OKN by using a method similar to that used previously with cats (Harris & Smith, 1990; Smith & Harris, 1991). Five normal adults viewed plaids composed of two drifting sinusoidal gratings arranged such that their individual directions of drift were 60 deg or more from the direction of coherent motion of the overall pattern. Physiological evidence indicates that under monocular viewing, nasalward coherent motion gives advantage to any crossed subcortical contribution while temporalward coherent motion minimizes it. We recorded horizontal eye movement by infrared reflection and asked subjects to report the perceived direction of motion.

During both binocular and monocular viewing, the direction of the slow phase of OKN fell closer to the direction of coherent movement than to that of the oriented components. Monocular viewing produced no nasal-temporal asymmetries in the influence of coherent motion on the direction of OKN. This suggests that in humans the influence of coherent motion is mediated primarily by cortical mechanisms and, unlike in cats, with little or no involvement of subcortical mechanisms in the generation of horizontal OKN.

Keywords: Eye movements, Optokinetic nystagmus, Motion perception, Cortical mechanisms, Plaids, Human adults

Introduction

The vestibulo-ocular reflex and its visual counterpart optokinetic nystagmus (OKN) are fundamental to all aspects of vision. They minimize the blurring of the retinal image that would otherwise be caused by the continual movements of the head in a stationary world by generating compensatory eye movements. OKN can be elicited experimentally in the absence of any head movement by movement of the images in the visual field. These eye movements have a characteristic pattern of so-called slow, compensatory phases interrupted by fast, resetting phases. This paper addresses the mechanism by which the slow phase is matched in direction and velocity to the movement of the stimulus.

The slow phase of human OKN comprises two elements: fast and slow build-up components. The initial part of the response is a rapid increase in the slow-phase velocity of the eyes in following the motion. This is the fast build-up component. The fast build-up phase of OKN is difficult to distinguish from smooth pursuit and, in fact, pursuit and fast build-up OKN might not actually be different. Both are mediated *via* cortical pathways and, in monkeys and humans, both are likely to share

some of the same cerebral neural circuitry (Pola & Wyatt, 1985; Carpenter, 1988; Tusa & Zee, 1989). If the OKN stimulus persists, eye velocity continues to build up more slowly to a plateau. This is the slow build-up component of OKN. For full-field motion, the fast build-up component (with its overtones of smooth pursuit) dominates the OKN response in humans, the slow build-up component dominates the response of rabbits and cats, and both components are equally evident in the response of monkeys. Nevertheless, in all these species, both components contribute to the steady-state slow phases of OKN.

In every species studied, the pretectal nucleus of the optic tract (NOT) and the dorsal terminal nucleus (DTN) of the accessory optic system play a central role in the generation of the slow build-up component of horizontal OKN (reviewed in Simpson, 1984). In cats and monkeys, neurons of the right NOT-DTN respond preferentially to motion in the rightward direction and those of the left NOT-DTN to leftward motion (Hoffmann & Distler, 1986). Electrical stimulation of these cells indicates that each NOT-DTN generates eye movements only in the direction to which its neurons are visually responsive (e.g. Schiff et al., 1988).

The NOT-DTN of cats and monkeys receives visual inputs both directly from the retina and indirectly *via* the cortex (see Grasse & Cynader, 1991). In both cats and monkeys, the subcortical and cortical pathways are each sufficient to mediate hor-

Reprint requests to: Laurence R. Harris, Department of Psychology, York University, Toronto, Ontario, M3J 1P3 Canada.

horizontal OKN to binocularly viewed stimuli or to monocularly viewed stimuli that move nasalward (leftward through the right eye and rightward through the left eye) but a cortical pathway is necessary for OKN to monocularly viewed stimuli that move temporalward (cats: Wood et al., 1973; Harris et al., 1980; Hoffmann, 1983; Montarolo et al., 1981; Strong et al., 1984; monkeys: Kato et al., 1986; Zee et al., 1987). Nonetheless, there appear to be important differences between cat and monkey in the strength of the cortical influence on NOT-DTN. First, in the monkey, 70% of cells in the NOT-DTN do not receive a direct retinal input at all and thus instead must receive their visual input exclusively from elsewhere; in the cat all NOT-DTN cells receive a direct retinal input (Hoffmann & Shoppmann, 1981; Grasse & Cynader, 1984; Hoffmann et al., 1988). Second, many more NOT-DTN cells are binocular in the monkey than in the cat (Hoffmann & Shoppmann, 1981; Grasse & Cynader, 1984; Hoffmann et al., 1988). Because of the sparse direct ipsilateral retinal projection in both species (reviewed in Hoffmann et al., 1988), binocularity implies cortical input (although monocular cells could still receive cortical input from the contralateral eye). Third, following cortical lesions, nasalward OKN appears to be more impaired in the monkey than in the cat (cat: Wood et al., 1973; monkey: Zee et al., 1987). Taken together these observations suggest a greater cortical influence on OKN in the monkey than on that of cats.

Hoffmann (1989) hypothesized that in cats, monkeys, and humans, horizontal OKN early in life is mediated entirely by the subcortical projections to NOT-DTN, which develop in the absence of visual experience. The cortical projections to NOT-DTN develop later and depend on normal binocular visual experience. After the cortical projections are established, the subcortical projections lose influence over NOT-DTN cells. Hoffmann (1989) speculated that this occurs to a small extent in cats, to a greater extent in monkeys, and almost completely in humans. Thus, increasing dominance of the cortex may be an evolutionary trend, culminating in an almost nonfunctional subcortical pathway in normal human adults.

Distinguishing the cortical and direct retinal contributions to OKN is an important goal. First, it is important for an understanding of the interactions between the subcortical, reflex control systems and the higher processes of the cortex. Second, it is relevant to understanding the phylogenetic development of the brain as well as its ontogenetic growth. Finally, it is important to understand the consequences of pathological conditions, such as strabismus or pattern deprivation. Such conditions affect not only the cortex (Blakemore & Hillman, 1977) but also its output to brain-stem systems, such as those that control OKN (Cynader & Harris, 1980). Disruption of eye movement control would, in turn, further degrade vision and hence potentially interfere further with the development of the cortex.

The relative influence of the cortical vs. subcortical pathways in the mediation of OKN can be distinguished in behavioral experiments by using plaid stimuli after the manner developed by Smith and Harris with cats (Harris & Smith, 1990; Smith & Harris, 1991). The plaids are composed of two overlapping moving gratings arranged such that the direction of motion of the individual oriented components is very different from that of the overall coherent pattern (Adelson & Movshon, 1982; Movshon et al., 1986). The oriented components can be detected only by orientation-selective spatial filters. Nonoriented motion detectors can respond only when the coherent pattern moves in their preferred direction. In cats, monkeys, and presumably

humans, the visual cortex is the first level capable of orientation selectivity. Thus, any influence of the oriented components of a plaid reveals an unequivocal contribution of the cortex. Moreover in cats, monkeys, and again presumably in humans, the direct retinal projection to the brain-stem OKN generator is functionally entirely crossed (cat: Hoffmann & Schoppmann, 1975; monkey: Hoffmann et al., 1988; see Simpson, 1984). Thus, functionally, the only direct retinal connection to the generator responsible for leftward slow phases is from the right eye. When stimuli are viewed monocularly, therefore, contributions from the direct retinal input to the brainstem will show strong nasal/temporal asymmetries. There is no reason to expect any such asymmetry in a pathway of cortical origin in adult cats, monkeys, or humans.

Any contribution of smooth pursuit to human OKN does not alter the logic for using plaids to distinguish cortical from subcortical contributions because mechanisms involved in mediating smooth pursuit (such as the dorso-lateral pontine nuclei, Bjaalie & Brodal, 1989; Mustari & Wallmann, 1988) receive their visual input primarily *via* the cortex (but see Aas, 1989; Wells et al., 1989). Thus, any monocular asymmetry in the response to plaids could only reflect the asymmetry of the direct visual input to the brain stem. A symmetrical monocular response in humans would indicate cortical domination, probably including the pathways that mediate smooth pursuit.

To investigate subcortical influences on the horizontal OKN system of humans, we showed plaids to normally sighted adults and recorded their horizontal eye movements and, for comparison, their judgements of the direction of motion. The plaids were selected such that the direction of motion of the oriented components was clearly distinguishable from the direction of motion of the coherent pattern. If the eyes followed the oriented components, this would reveal an important input from the cortex. Following the direction of coherent motion could indicate either that subcortical pattern detectors dominate the response or that the direction of the overall pattern has been deduced from the output of cortical orientation detectors (Movshon et al., 1986; Gizzi et al., 1990). These two alternatives can be distinguished by the results of monocular presentation which should give a bias to nasally directed movement if the response is dominated by the cells that form the direct retinal projection but which should have no effect if the response is based on cortically generated eye movements (see Smith & Harris, 1991, for a detailed explanation). A summary of some of the results of this study has been published previously (Harris et al., 1991).

Methods

Stimuli

The experimental stimulus was a plaid made up of two sine-wave gratings oriented at 15 deg to each other (see Fig. 1). The individual gratings had a contrast of 25% giving a contrast of 50% for plaids comprising the sum of two such gratings. The spatial frequency was 0.4 cycle/deg when viewed from 50 cm. One grating moved at 4.7 deg/s and the other at 9.2 deg/s, with a resultant coherent movement 60 deg away from the nearest oriented component at 18.4 deg/s. The control stimulus was a grating identical to one of the components of the plaid, moving at a velocity of 18.4 deg/s.

The plaid is an example of a type II plaid as described by Ferrera and Wilson (1990) because the direction of coherent mo-

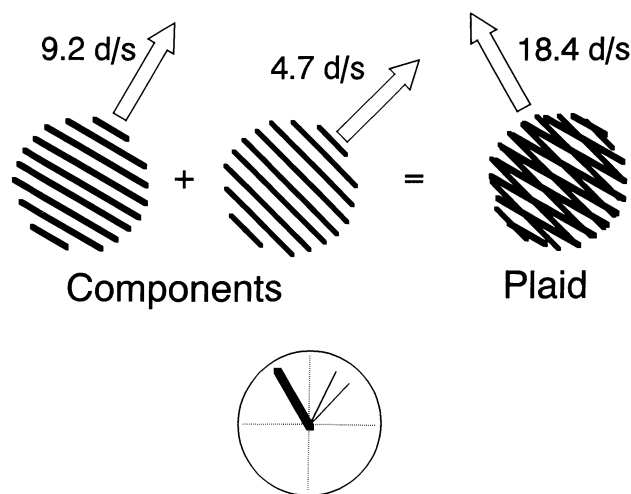


Fig. 1. Diagram showing the construction of the plaid used in this paper. The speeds of the components are shown above each grating and the speed of the resulting pattern can be calculated from a diagram of constraints. Note that the direction of coherent motion is 60 deg counterclockwise from the nearest component. This is called a type IIA plaid: "II" because the direction of coherent motion is outside that of the components (Ferrera & Wilson, 1990) and "A" because the direction of its coherent motion is displaced counterclockwise from the direction of motion of the oriented components (see text). A representation of the plaid is shown as an insert. The thick line represents the direction of the coherent motion, and the thinner lines represent the direction of motion of the components.

tion falls outside the direction of motion of the oriented components. We presented this plaid and its mirror image, each in various orientations (see Stimulus Presentation). (Using mirror images reveals the contribution of any directional biases.) To distinguish a plaid from its mirror image, we have called plaids in which the coherent pattern is displaced counterclockwise from the components "type A" plaids (illustrated in Fig. 1 and insert to Fig. 2A) and those in which the coherent pattern is displaced clockwise from the components "type B" plaids (see insert to Fig. 2B).

The stimuli were generated using a CARDIFF VISUAL SYSTEMS Constable Pattern Generator controlled by an AT PC computer. The patterns were presented on an HP1310A screen filling a circular aperture which subtended 35 deg at the viewing distance of 50 cm. The stimuli were the same as used with cats in Smith and Harris (1991), although for cats the viewing distance was closer (35 cm). A 35-deg stimulus produces OKN which appears almost indistinguishable from full-field presentation (Howard & Ohmi, 1984) and is certainly adequate to stimulate NOT cells in the monkey (Hoffmann & Distler, 1986; Mustari & Fuchs, 1989).

Subjects

The subjects were five adults ranging in age from 19 to 40 years (median age = 25 years). All had at least 20/20 vision in each eye when tested uncorrected at far and at near and all had normal stereopsis on the Titmus test. Each subject signed a consent form and was paid five dollars for participation.

Stimulus presentation

Each stimulus was presented for at least 20 s. Subjects were instructed to "stare straight ahead and keep the image in focus." Eye movements were recorded for a 16-s period, commencing about 2 s after viewing began. Then, before the stimulus was turned off, the subject was asked to judge its direction of motion as an "o'clock" such that 12 was straight up, 3 was to the right, etc. We rotated the stimuli (the plaid, its mirror image, and the single grating) in 15-deg steps and recorded the horizontal eye movements and judgements for each presentation. The particular orientations used for each subject are shown in the relevant figures. We interpolated the orientation of the plaid eliciting no horizontal eye movements.

Subjects viewed the series of plaids twice, once binocularly and once monocularly with the left eye. Single gratings were viewed only monocularly with the left eye. During monocular tests, the right eye was occluded with an opaque patch.

Analysis of eye movements

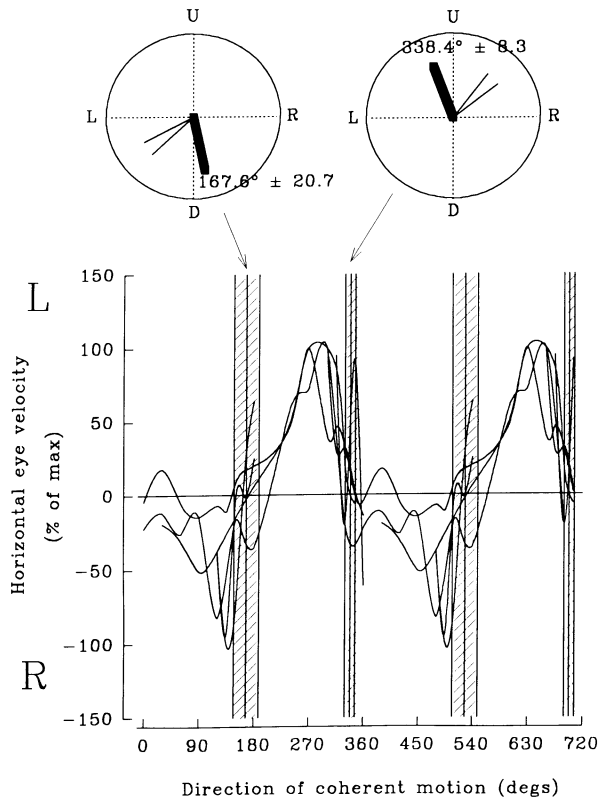
Horizontal eye movements were measured by an infrared reflection technique, recorded through an analogue-to-digital converter and stored on disc for later analysis. Horizontal eye movement calibration was done by asking the subject to look at points 10 deg left and right of straight ahead. To analyze the response to plaids, the velocity of four representative slow phases were measured. Consecutive slow phases were selected from the middle of the recording period; if no slow phases could be identified clearly, the average velocity between saccades was measured. The slow-phase velocity was obtained by measuring the distance between eye position sampled near the beginning of a slow phase and eye position sampled near the end of that same slow phase. Dividing by the time between samples yielded the average velocity (in deg/s). The mean of these four velocity measures was then expressed as a percentage of the maximum velocity recorded from that subject in that condition (e.g. monocular type A plaids) and plotted as a function of the direction of the coherent motion of the plaid. An estimate of the direction of the plaid that would yield a horizontal eye velocity of zero was obtained by measuring where a spline interpolation through these data points crossed zero. Examples of such plots are given in Fig. 2, and explained further in the next section.

Results

Binocular presentation of plaids: eye movements

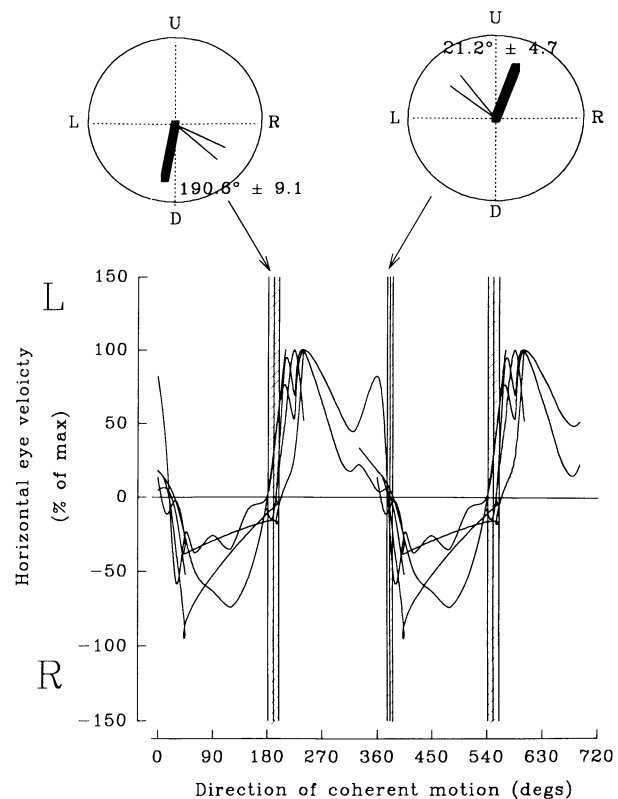
Plaids evoked a vigorous horizontal nystagmus when viewed binocularly. The velocity of this horizontal nystagmus was affected by the orientation of the plaid. The average peak velocity was $15.2 \text{ deg/s} \pm 1.29 \text{ (s.e.)}$. This represents a gain (eye velocity/stimulus velocity) of 0.82 with respect to the coherent speed of the plaid (18.4 deg/s) and is faster than either of the components (4.7 and 9.2 deg/s). Fig. 2 shows the normalized velocities for all subjects viewing type A plaids (Fig. 2A) and their mirror images, type B plaids (Fig. 2B). The horizontal component of all aspects of the plaids' motions (that of the coherent pattern and each of the two components) are related to the orientation of the plaid. For convenience, we have represented the orientation of the plaid by the direction of motion of the coherent pattern with 0 defined as moving straight up, 90 mov-

BINOCULAR: TYPE A PLAIDS



A

BINOCULAR: TYPE B PLAIDS



B

Fig. 2. The relative horizontal slow-phase eye velocity evoked in response to plaids presented at various orientations whilst viewing binocularly. The vertical axis represents horizontal eye velocity plotted as a percentage of the maximum response for each subject. Up is left. The horizontal axis is the orientation of the plaid, taken for convenience as the direction of the coherent pattern motion. 0 = straight up, 90 = rightward, 180 = straight down, etc. The data lines are spline interpolations through the individual subject's data. For clarity, the entire graph has been plotted twice over along the horizontal axis (0 = 360, 90 = 450, etc.). The means of the points where the plots cross zero velocity (zero horizontal eye velocity) are each marked by a vertical line flanked by shading out to vertical lines at ± 1 s.d. Above, as inserts in the format explained in Fig. 1, are shown the plaids corresponding to the orientation of the mean direction yielding no horizontal eye movements. A: The responses to type A plaids, in which the direction of the coherent pattern motion is displaced counterclockwise from the direction of the components. B: The response to type B plaids which are the mirror image of type A plaids.

ing rightward, 180 straight down, etc. For clarity, we have plotted the entire graph twice along the X axis so that 0 deg is equivalent to 360 deg, 90 deg to 450 deg, etc. The data for each subject are quite noisy and only roughly approximate a sinusoidal function. The direction of motion of the plaid that evokes a horizontal velocity of zero can be estimated from where the spline interpolation crosses zero. The average crossing is shown by the vertical lines, flanked by ± 1 s.d. Above are shown the four plaids (two type A: Fig. 2A and two type B: Fig. 2B) that correspond to these orientations associated with no horizontal nystagmus. Careful inspection of the subjects as they watched plaids of close to these orientations showed that they produced vertically directed nystagmus.

For plaids that produced no horizontal eye movements, neither the direction of coherent motion nor that of the components was actually vertical. These directions straddled the vertical (see inserts to Fig. 2). The mean distance away from vertical

was 16.5 deg (s.d. ± 5.0) for the direction of coherent motion and 43.5 deg (s.d. ± 5.0) for the direction of the nearest component. Clearly the direction of coherent motion dominated the response but did not account for it completely.

Binocular presentation of plaids: judgements

Fig. 3 shows the subjects' judgements of the direction of motion: Fig. 3A for type A plaids and Fig. 3B for the mirror image, type B plaids. To assess the direction of the plaid judged to move straight down or straight up, we used an averaging method similar to that used for the eye movements to assess the direction of plaid corresponding to a judgement "6 o'clock" (moving straight down) and a judgement "12 o'clock" (moving straight up). Subjects frequently estimated to the nearest half-hour, corresponding to an accuracy of ± 7.5 deg. Like the eye movement data, the judgements indicate that the direction

BINOCULAR: TYPE A PLAIDS

BINOCULAR: TYPE B PLAIDS

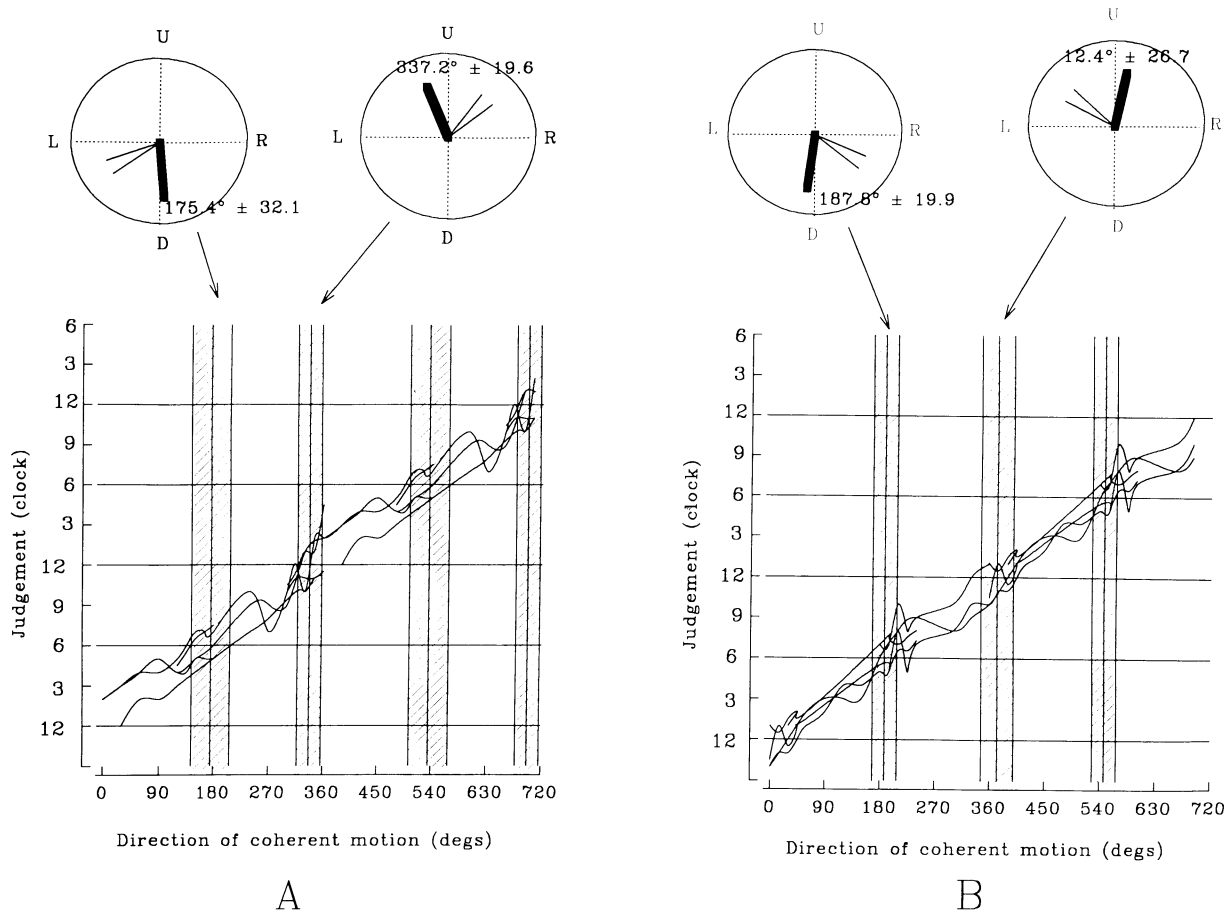


Fig. 3. Plots of the direction in which plaids were judged to be moving (reported as clock numbers) against the direction of the plaid when viewed binocularly. As in Fig. 2, the direction of the plaid is plotted, for convenience, as the direction of the coherent pattern motion. As for Fig. 2, the entire graph has been plotted twice for clarity. Note that both the "judgement" and the "direction of plaid" axes are circular. The mean direction of the plaid that is judged as moving straight up (12 o'clock) and straight down (6 o'clock) have been assessed in the same way as the eye movement zero crossings. Here they correspond to the points at which the data spline interpolation crosses the 12 or 6 lines. The plaids corresponding to these estimates are shown as inserts above. Type A (A) and type B (B) plaids are plotted separately as they were in Fig. 2.

of motion of the coherent pattern dominates the response but the components do have some influence (compare the inserts in Figs. 2 and 3). For plaids judged to move straight up or straight down, the mean distance from vertical was 12 deg (s.d. ± 7) for the direction of coherent motion and 48 deg (s.d. ± 7) for the direction of the nearest component.

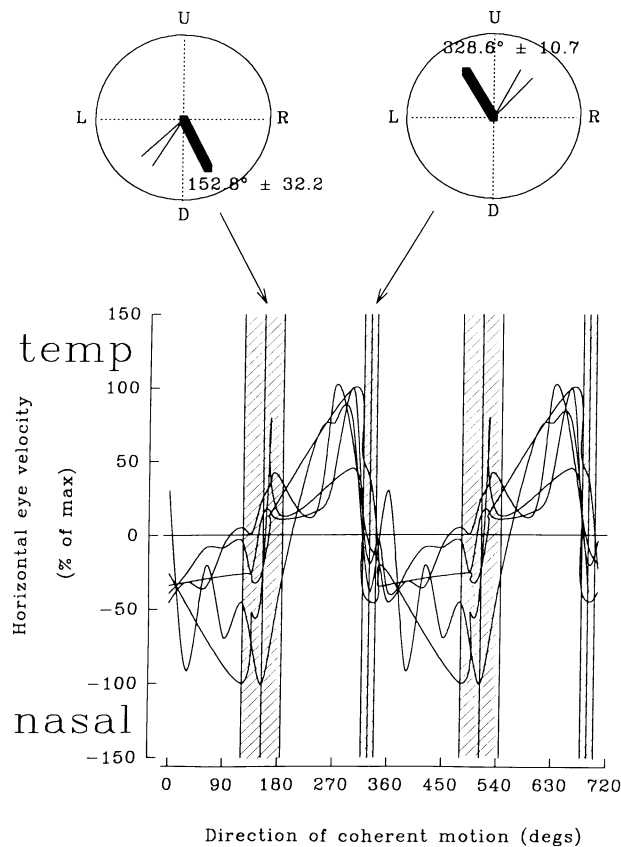
Monocular presentation of plaids: eye movements

Fig. 4 summarizes the horizontal eye movements evoked by plaids viewed monocularly. The average peak velocity of horizontal OKN was $10.5 \text{ deg/s} \pm 1.2 \text{ s.e.}$ which represents a gain (eye velocity/stimulus velocity) of 0.57 with respect to the coherent plaid and is faster than either of the components (4.7 and 9.2 deg/s). The peak velocity measured during monocular viewing was significantly slower than when viewing was binocular ($t_{18} = 2.53$, $P = 0.02$, 2-tailed). This monocular-binocular difference cannot have been caused by difficulties of calibrat-

ing the infrared recording system since inaccuracies would affect both conditions.

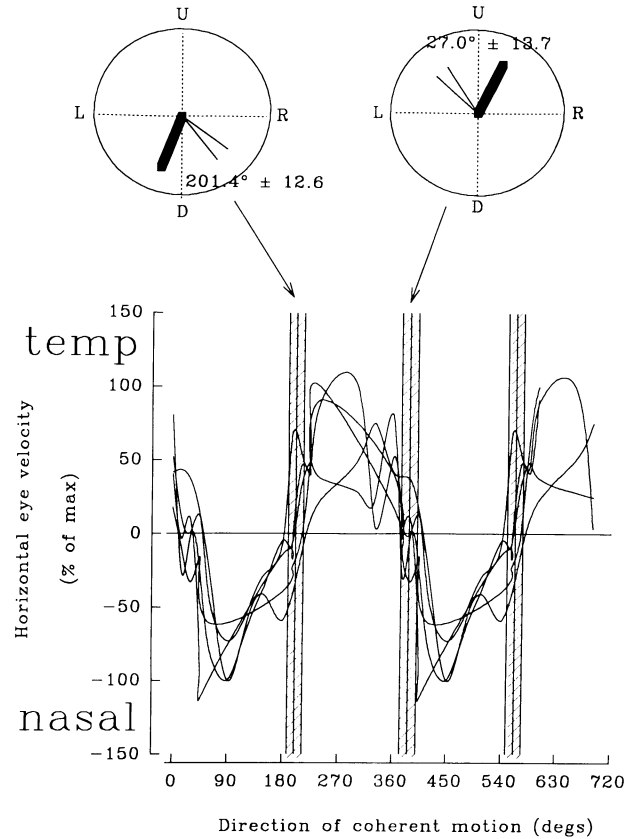
The significance of monocular viewing is that plaids can be created in which the coherent motion moves nasalward but the oriented components move temporalward, or *vice versa*. Thus in Fig. 4A, the downwardly directed plaid giving no horizontal OKN and, in Fig. 4B, the corresponding upwardly directed plaid are associated with a nasally moving coherent motion and temporally moving oriented components. But for the upwardly directed plaid shown in the insert of Fig. 4A and the downwardly directed plaid of Fig. 4B, the coherent pattern is moving in the temporal direction and the oriented components in the nasal direction. We assume that in humans, as in cats and monkeys, the direct subcortical projection does not respond to the oriented components of the plaid and favors nasalward coherent motion over temporalward coherent motion (see Introduction). We also assume that the cortical projection can respond both to the oriented components and to the coherent motion with

MONOCULAR: TYPE A PLAIDS



A

MONOCULAR: TYPE B PLAIDS



B

Fig. 4. The relative horizontal slow-phase eye velocity evoked in response to plaids presented at various orientations while viewing monocularly. The format is exactly as for Fig. 2. Since viewing is through the left eye, leftward slow phases can now be described as temporally directed (away from the nose) and rightward slow phases are nasal (towards the nose). The plaids corresponding to orientations of plaids evoking no horizontal nystagmus are shown as inserts above. A: The response to type A plaids. B: The response to type B plaids.

no nasal/temporal asymmetries. Thus, if there is a direct retinal contribution to the mediation of OKN, the influence of the coherent motion on the response should increase for nasalward coherent motion and decrease for temporalward coherent motion.

In fact, comparison of the binocular and monocular eye movement data (c.f. Figs. 2 and 4) reveals no consistent differences in direction between them. We used an ANOVA to compare the distance from true vertical of the coherent pattern eliciting no horizontal OKN under binocular vs. monocular viewing conditions for type A vs. type B plaids moving either upward or downward. There were no significant differences for binocular vs. monocular viewing nor for upward vs. downward motion (both P s > 0.10). There was a significant difference between type A and B plaids ($P < 0.001$) in the direction that would be expected if the influence of coherent motion predominated.*

*Although there was a significant difference between type A and B plaids for both monocular and binocular viewing (both P s ≤ 0.001), there was also an uninterpretable interaction.

To determine whether individual subjects showed differences between binocular and monocular viewing in the influence of coherent motion on the velocity of horizontal eye movements, we used a sign test for each subject to compare the two conditions for each direction of stimulus motion. We performed these analyses separately for trials where the monocularly viewed pattern moved nasalward vs. temporalward.† In each comparison, we assigned a positive value if the influence of coherent motion was greater for binocular than monocular viewing and a negative value if the influence of coherent motion was greater for monocular than binocular viewing. There were no significant differences in four of the five subjects, but for the remain-

†We used a sign test rather than a Wilcoxon test for the analysis of eye movements because we wanted to give an equal weight to all trials regardless of the direction of motion. Because we measured only horizontal eye velocity, trials with the direction of motion closer to horizontal would have larger horizontal eye velocities than those closer to vertical. But there was no such bias in the judgement data because subjects could give judgements in any direction. Therefore we analyzed the judgements with a Wilcoxon test.

ing subject, the direction of coherent motion had a greater influence on eye movements for binocular than for monocular viewing ($P < 0.01$ for nasalward pattern movement; $P = 0.058$ for temporalward motion). However, in no subject was there a differential influence of the coherent motion for nasalward vs. temporalward movement (all P s > 0.10), a finding which suggests little or no influence of the direct subcortical projection on the mediation of horizontal OKN.

Monocular presentation of plaids: judgements

We analyzed the distance from true vertical of the direction of the coherent pattern for plaids judged to be moving vertically. An ANOVA indicated that, as with eye movements, there were no significant differences for binocular vs. monocular viewing nor for upward vs. downward motion (both P s > 0.10). There was a significant difference between type A and type B plaids, but only for upward motion (interaction: $P < 0.02$). The lack of a significant difference for downward motion is likely to be caused by the greater variability in judgements for downward than for upward motion, particularly for type A plaids (c.f. Figs. 3 and 5).

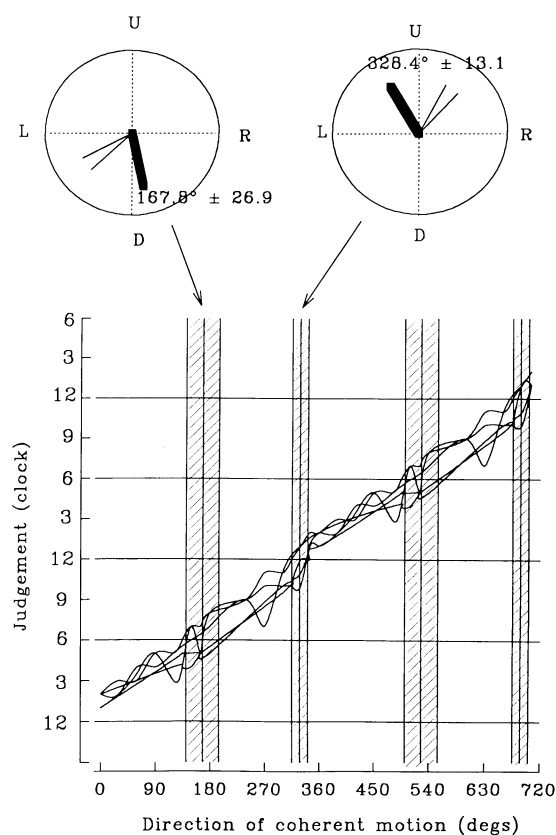
To determine whether individual subjects showed differences

in the judged direction of motion for binocular vs. monocular viewing, we used a modified Wilcoxon test of matched pairs comparing the two conditions for each subject. For each comparison, we assigned a positive value to the difference score if the influence of coherent motion was greater for binocular than monocular viewing and a negative value if the opposite was true. There were no significant differences in three of five subjects. In the remaining subjects, the direction of coherent motion had a greater influence on judgements for binocular than monocular viewing, in one subject when the monocularly viewed pattern moved nasalward and in the other subject when it moved temporalward (both P s = 0.02). In no subject was there a differential influence of coherent motion for nasalward vs. temporalward movement (all P s > 0.05). Thus for judgements, as for eye movements, coherent motion sometimes has less influence for monocular than for binocular viewing but its influence is always comparable for nasalward vs. temporalward motion.

Gratings: eye movements

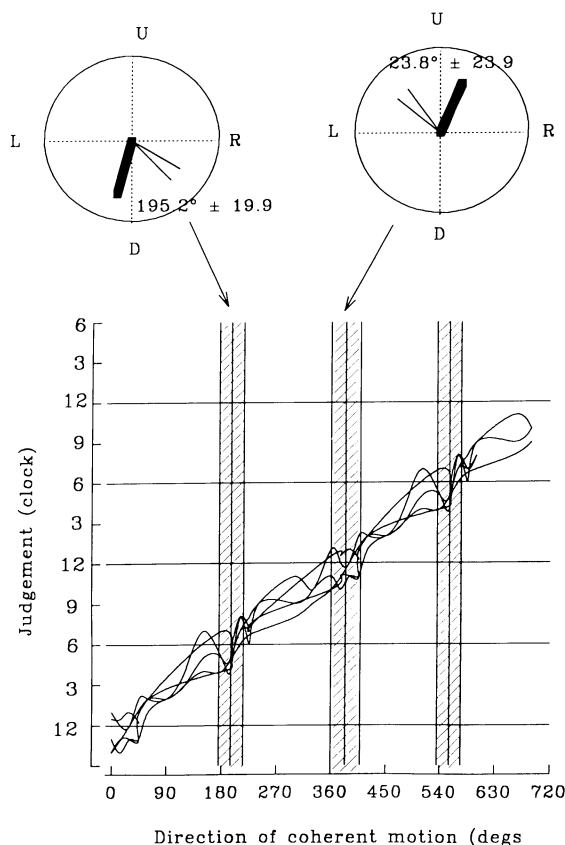
As a control, we had four subjects view monocularly single gratings moving at the same speed as the coherent pattern (18.4 deg/s). The results for eye movements are summarized in Fig. 6.

MONOCULAR: TYPE A PLAIDS



A

MONOCULAR: TYPE B PLAIDS



B

Fig. 5. Plots of the direction in which plaids were judged to be moving (reported as clock numbers) against the direction of the plaid when viewed monocularly. Format is as for Fig. 3 with the temporal-nasal features of Fig. 4. A: Obtained using type A plaids. B: Obtained using type B plaids.

The average peak velocity was 12.4 deg/s which represents a gain (eye velocity/stimulus velocity) of 0.67 ± 0.07 , similar to that reported in previous comprehensive studies of simple stimuli (e.g. van den Berg & Collewijn, 1988). These control peak eye velocities fell between the values obtained from the monocular and the binocular plaid data. There was a slight rightward advantage in the maximum speeds of the horizontal eye velocity: all of the "maximum" responses occurred when the gratings were moving to the right (nasally). And, as shown in the inserts to Fig. 6, the gratings that produced no horizontal eye movements had slight leftward (temporal) biases for both downwardly and upwardly directed gratings. Sign tests indicated that three of the four subjects showed no significant nasal/temporal biases in their response to single gratings (all P s > 0.10). The fourth subject had significantly greater horizontal eye velocity for nasalward than for temporalward motion ($P < 0.01$). Nonetheless, any such constant bias would affect equally eye movements to plaids under monocular and binocular viewing conditions. In addition, despite this bias, we did not find a larger influence of the pattern when it moved nasalward than when it moved temporalward.

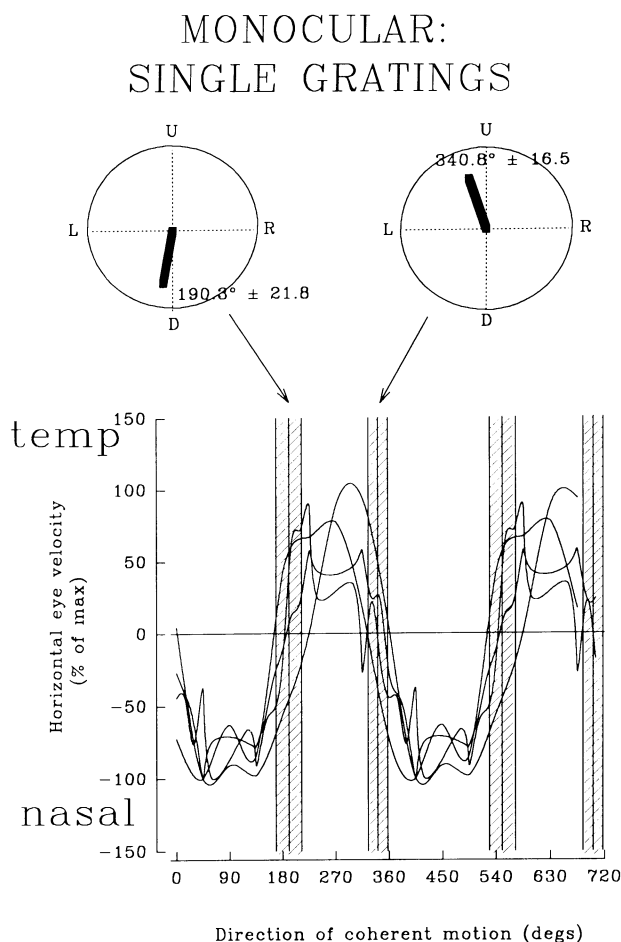


Fig. 6. The relative horizontal slow-phase eye velocity evoked in response to single gratings presented at various orientations whilst viewing monocularly through the left eye. The format is exactly as for Fig. 2. The inserts show the direction of the grating that produced no horizontal optokinetic nystagmus.

Gratings: judgements

The direction of a single-moving grating was judged quite accurately. Fig. 7 reveals accurate judgements with very little scatter and no bias like that found in the eye movements (Wilcoxon tests, all P s > 0.10).

Correlations of judgements and eye movements

If both perceptions and eye movements are controlled by the same system, we would anticipate a tight coupling between the direction of eye movements and of judgements. An ANOVA revealed no noteworthy differences between the average judgements of a plaid's direction as vertical and the orientation that evoked a corresponding pattern of eye movements.‡ But to check the correlation between eye movements and judgements

‡Like the previous analyses, this ANOVA revealed a significant difference between type A and B plaids in the direction indicating a stronger effect of the coherent motion than of the oriented components, especially when the stimuli were viewed monocularly (type A vs. B: $P < 0.03$; interaction: $P < 0.05$).

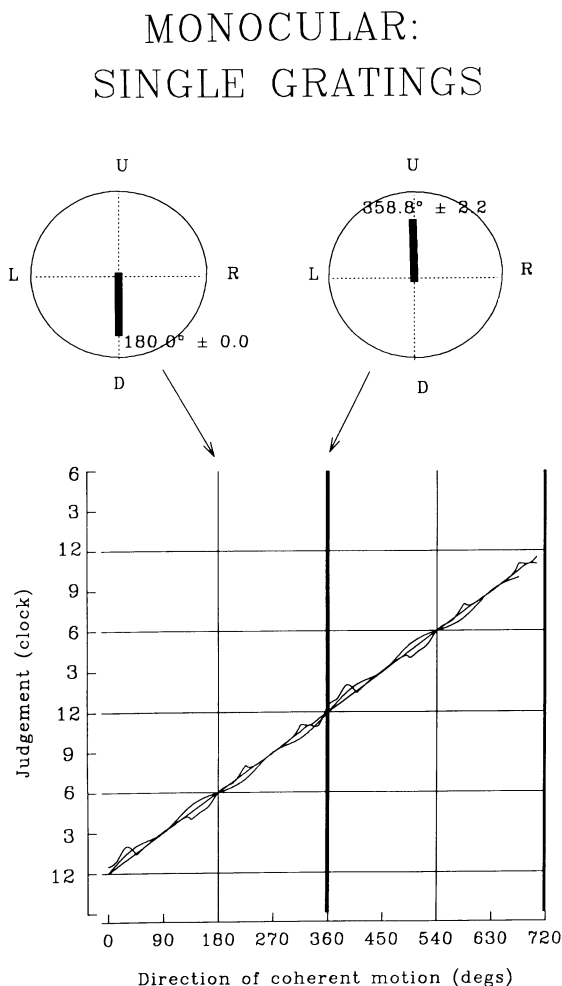


Fig. 7. Plots of the direction in which gratings were judged to be moving (reported as clock numbers) against the direction of the grating when viewed monocularly through the left eye. Format is as for Fig. 3.

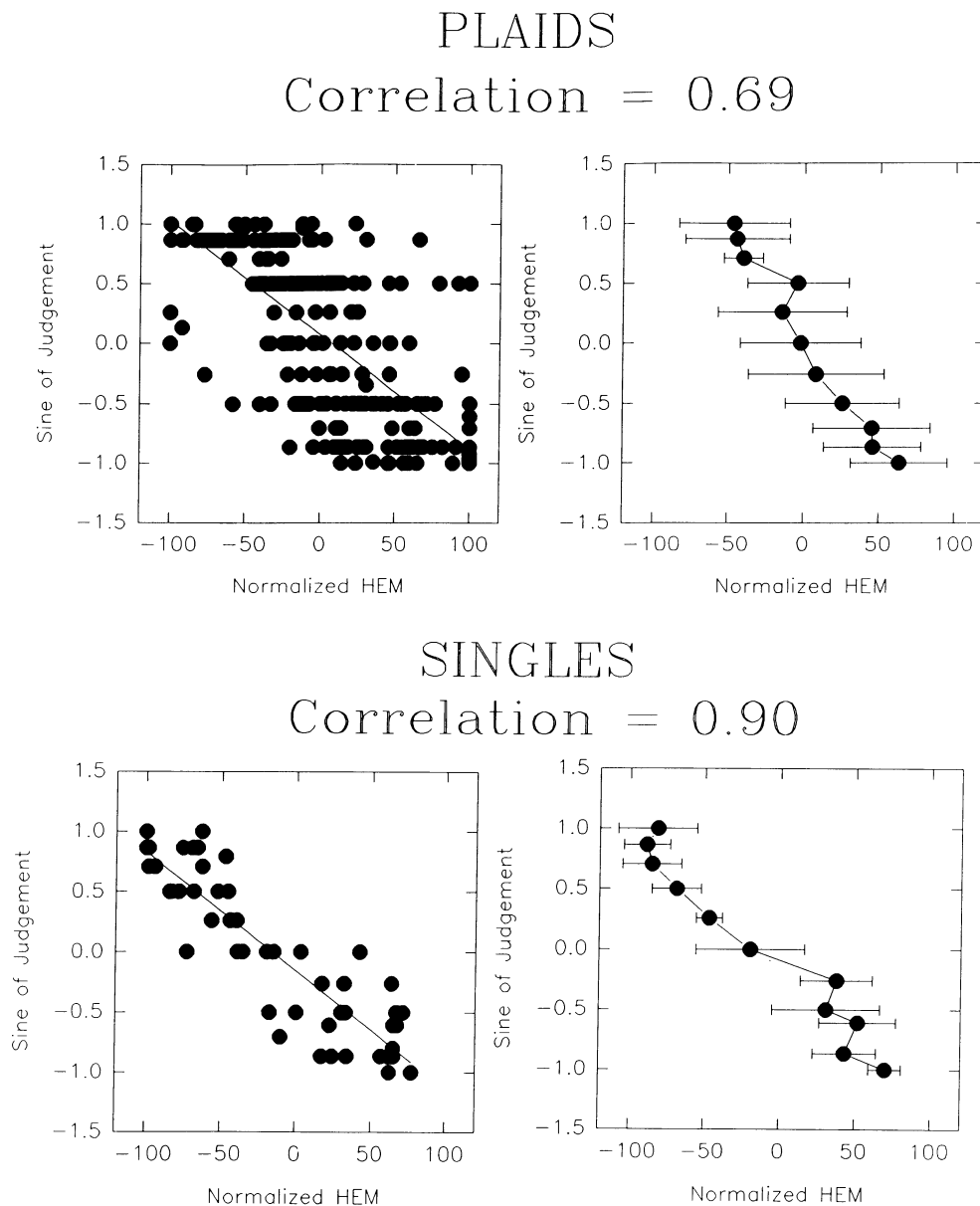


Fig. 8. The correlation between the sine of the judgement and the corresponding horizontal eye movement (HEM) normalized to a maximum of 100. The upper panels are the correlations for plaid data and the lower panels are the correlations for data obtained from single gratings. The left panels show each data point along with the regression lines and the right panels show means ± 1 s.d. The regression coefficients of the regression lines are 0.69 for plaids and 0.9 for single gratings.

from trial to trial, we transformed the judgement scale so that, like the normalized horizontal eye movements, it was sinusoidal. A simple linear-regression analysis of these transformed data revealed a correlation of 0.9 for single gratings and of 0.69 for plaids. These are illustrated in Fig. 8. A Fisher z_r transformation indicated that the correlation for single gratings was significantly better than that for plaids ($z = 3.98$, $P < 0.0001$, 2-tailed).

Discussion

This paper presents the following main findings about the eye movements elicited by type II plaids in human adults:

1. The direction of the evoked eye movements falls closer to the direction of motion of the coherent pattern than to the direction of motion of the oriented components under our stimulus conditions.
2. Plaids are followed at a significantly higher velocity when viewed binocularly than when they are viewed monocularly.
3. The velocity of the evoked eye movements exceeds that of either of the components and more closely matches the speed of the coherent pattern.
4. The influence of the coherent pattern does not differ significantly for nasalward vs. temporalward motion.
5. Although there are no significant differences overall between judged direction of motion and the direction of optokinetic nystagmus, the trial-to-trial correlation is only moderate.

Validity of the measures

We used an infrared reflection technique which recorded only horizontal eye movements. Nonetheless, by rotating the stimuli, we were able to interpolate the point where there were no

horizontal eye movements. For single gratings the strong correlation between judgement of the direction of motion and eye movement responses indicates that this method of interpolation was valid.

Eye movements evoked by plaids will introduce an additional movement vector to the retinal image. The consequences of this for a plaid are explained in the Appendix and Fig. 10. We considered the possibility that shifts in the direction of the plaid on the retina as a result of ongoing eye movements might explain the shifts in the judgement data (see Figs. 3 and 5). In other words, is a plaid judged as moving in a particular direction (e.g. 12-o'clock) when it actually is moving in that direction on the retina, although not on the screen? The Appendix shows that the coherent direction of a plaid is always in fact moved away from the vertical by the addition of the downwards velocity vector caused by upwards eye movement. The peak horizontal velocities for monocular and binocular plaids were 10.5 and 15.2 deg/s, respectively. Fig. 10B shows that the consequence of adding 10.5 deg/s is to reduce the velocity of the components, almost nulling one (shifting it from point a1 to point a2) and actually reversing the other (from point b1 to point b2). This has the effect of swinging the coherent direction from 328 deg (c1) to 297 deg (c2). The consequence of adding 15.2 deg/s is to reverse both components (to points a3 and b3) and to swing the coherent direction almost horizontal (to 271 deg, point c3).

Neither perceptual judgements nor eye movement control can be concerned with retinal image motion except in the context of knowledge about eye movements. When viewing a moving stimulus with a gain close to unity, the pattern is not seen as stationary, even though the image is (essentially) stabilized. And of course eye movements continue to be generated by a system that must take into account not only the relatively small retinal slippage but also the ongoing eye movements. The situation appears, initially, more complex for plaids because the entire visual structure depends on the relative velocities of the components. And these are, indeed, altered on the retina (see Appendix). Consider the retinal events whilst viewing the plaid of Fig. 10B that evoked upward-directed eye movements of 15.2 deg/s: on the retina, both components are moving *down* and to the left and the coherent direction is horizontal (Fig. 10B). Thus, in this example the directions of subjects' eye movements and judgements do not even fall between the direction of *retinal* coherent motion of the plaid and its components. Our data show that both for perceptual judgements and for eye movement control, the brain takes the movements of the eye into account when processing type II plaids and makes judgements and controls eye movements based on an internal representation of the external stimulus – not the retinal image alone. This result shows very clearly the dominant role of the cortex in the generation of human OKN.

Cortical vs. subcortical influences on optokinetic nystagmus

The brain-stem ultimately controls optokinetic nystagmus. The question that this experiment illuminates is which inputs to this machinery are active in normal human adults.

A single grating moving in a particular direction evokes OKN in the same direction as the stimulus, that is with the appropriate amounts of vertical and horizontal nystagmus. We assume that the amount of horizontal nystagmus is reflected in corresponding activity in one or other NOT. We estimated the direction of motion of plaids that evoked no horizontal nystagmus.

We assume that when no horizontal nystagmus occurs, this corresponds to no activity above the spontaneous level occurring in either NOT. The direction of the coherent motion of our type II plaids which evoked no horizontal nystagmus was 26–27 deg from vertical (see data Fig. 4 and summary Fig. 9). In this position, the coherent motion has its horizontal component in the opposite direction to that of the oriented gratings. A single grating moving at 26–27 deg from vertical evokes eye movements with an appropriate amount of horizontal nystagmus. But our plaids with coherent motion at 26–27 deg evoked no such horizontal nystagmus. This implies that the NOT's drive to produce horizontal eye movements in response to the horizontal component of the coherent motion was cancelled by a simultaneous drive in the opposite direction evoked by the motion of the oriented elements of the plaid. The strength of the contributions of the coherent motion and the motion of the oriented components vary both with their direction (being proportional to the sine of their angle with vertical) and with their relative effectiveness or weighting. A relatively strong effectiveness of

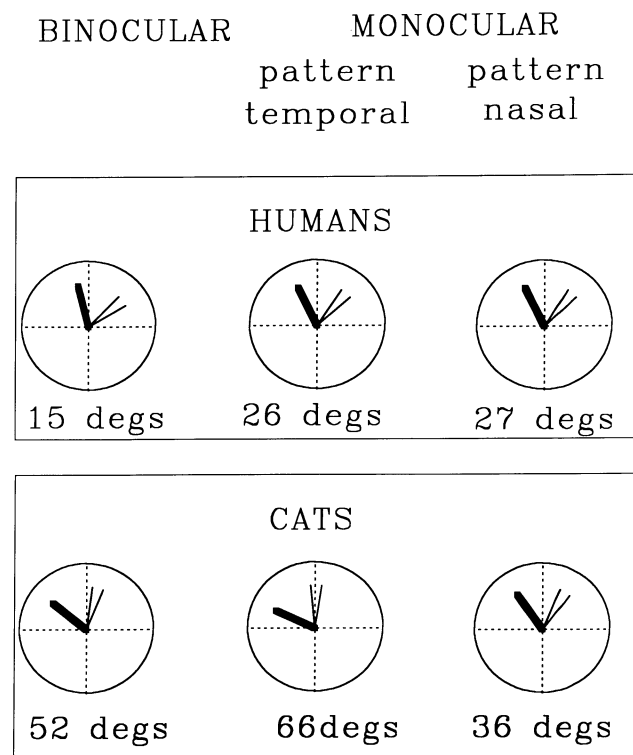


Fig. 9. A comparison of plaids that evoke no horizontal optokinetic nystagmus for binocular and monocular viewing conditions in humans (upper panel) and in cats (lower panel). Numbers below each circle represent the mean deviation from vertical of the direction of coherent motion. For humans, the mean deviation for binocular viewing was calculated by averaging the four deviations illustrated in Fig. 2: Type A and B plaids moving downward and upward. The mean deviations for monocular viewing were calculated by averaging the two deviations for temporal motion and the two deviations for nasal motion illustrated in Fig. 4. The mean deviations for cats were extracted from Smith and Harris (1991). Eye movements are all much closer to the direction of the coherent motion for the human than for the cat. There were not changes with monocular vs. binocular viewing or with temporal vs. nasal motion in humans, but the changes were pronounced in the cat (see text).

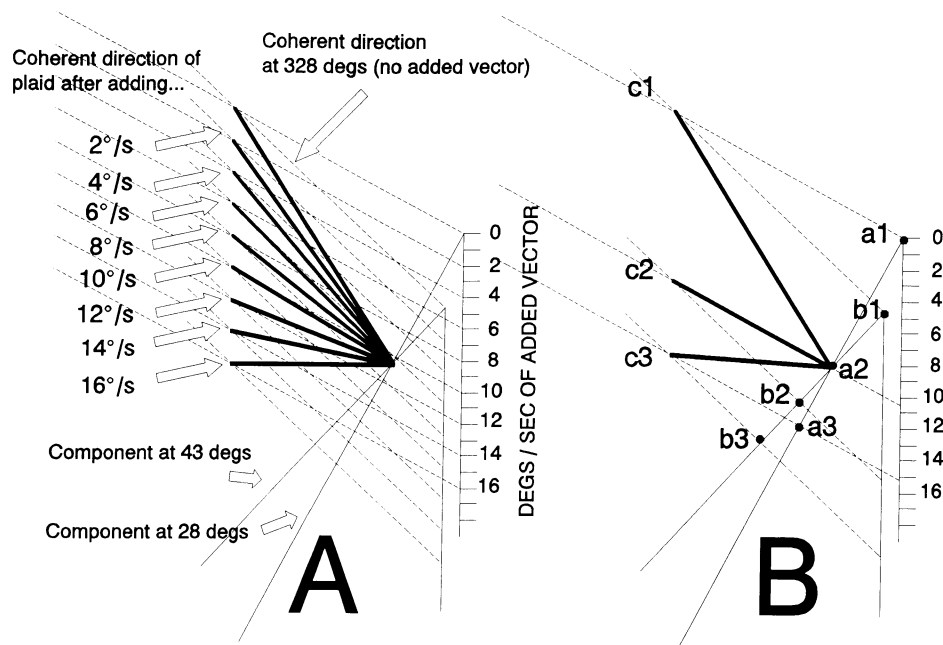


Fig. 10. The effect of adding a velocity vector to a moving plaid. Panel A shows a vector diagram of a type A plaid used in this study, oriented as shown in Figs. 4 and 5 (coherent direction at 328 deg, components at 43 and 28 deg) so as to evoke no horizontal eye movements and to be judged as moving at 12 o'clock. The solid lines are vectors which represent the motion of the components (thin lines) and the coherent motion (thick lines). The direction of these vectors from the center represents the direction of motion and their length is proportional to their velocity. The dashed lines are the lines of constraint (see Adelson & Movshon, 1982) which determine the coherent direction that results from the components. Also shown in panel A is the family of plaids produced by adding downwards-directed velocities such as introduced by an upwards eye movement. The added velocity vector alters the speed of each of the gratings that make up the original plaid by the component of the added vector along the direction of motion of that grating. The direction of coherent motion for each plaid that results from these new grating speeds is equivalent to a vector sum between the original coherent direction and the added vector. Panel B illustrates the three plaids that are obtained with (1) no added velocity, i.e. the plaid as presented on the screen: coherent = c1, components = a1, b1; (2) an added velocity of 10.5 deg/s, i.e., as found on the retina during an upwards eye drift at that velocity: coherent = c2, components = a2, b2; and (3) an added velocity of 15.2 deg/s: coherent = c3, components = a3, b3. See Appendix.

the coherent motion will shift the balance point closer to the position where the coherent motion is vertical. Conversely, if the oriented components dominate, the plaid evoking no horizontal nystagmus will be rotated into the position where the oriented components are closer to the vertical. If both motions are equally effective, the balance point is achieved when they are symmetrical about vertical.

We found that with monocular viewing, both NASAL and TEMPORAL coherent movement were balanced by the same contribution from the oriented components (i.e. by the same orientation of the plaid: 27 deg). We interpret this as indicating that the effectiveness of the coherent motion is the same irrespective of whether it is nasally or temporally directed. The influence of the coherent motion is thus unlikely to originate from the direct retinal pathways since the direct retinal pathways are functionally highly asymmetric (assuming that the cortical and subcortical pathways function similarly in monkeys and humans: see Introduction) and would lead to a greater effectiveness of nasalward as opposed to temporalward coherent motion as was found in the cat (Harris & Smith, 1990; Smith & Harris, 1991). We therefore conclude that the dominant visual input to the brain-stem horizontal optokinetic generator is from the cortex.

Because the direction of eye movements was closer to the direction of coherent motion than to that of the oriented com-

ponents, we conclude that the cortical influence represents primarily the output of a stage that has deduced the overall direction of coherent motion from the output of earlier oriented channels. These earlier oriented channels may themselves still play a small role in determining brain-stem responses, since neither the eye movements nor the judgements were consistent with *only* the direction of the coherent motion. This indicates some influence of a system that can extract information about the one-dimensional oriented components of the plaid. Simpson and Swanston (1991), using type I plaids, also provide evidence consistent with our conclusion that human OKN is influenced primarily by the coherent motion of a plaid. Finally, there are some differences between binocular and monocular viewing. Binocularly viewed plaids evoked faster eye movements than those evoked during monocular viewing. Also, in a few subjects, there was a greater influence of the coherent pattern when it was viewed binocularly than when it moved either temporalward or nasalward. These findings suggest that cells where the coherent motion is deduced may be predominantly binocular.

Comparison of horizontal OKN generation in humans and cats

The only other behavioral study addressing the question of cortical vs. subcortical influences on optokinetic nystagmus was

done on cats (Harris & Smith, 1990; Smith & Harris, 1991). The most obvious difference between the human and the feline responses to plaids is that the oriented components dominate the response in the cat but not in the human. For the cat viewing plaids binocularly, the direction of OKN is only 8 deg away from the nearest oriented component as opposed to 45 deg for humans (compare the first column of circles in Fig. 9).

When viewing is monocular, the cat's response is much affected, with the influence of the coherent pattern increased for nasalward motion and reduced markedly for temporalward motion. As discussed in the Introduction, such an asymmetry implicates the involvement of the direct subcortical pathways in the generation of cats' OKN. In humans, the direction of coherent motion dominates eye movement responses whether viewing is binocular or monocular and whether the direction of coherent motion is nasalward or temporalward. As discussed in the Introduction, this suggests little or no involvement of the direct subcortical pathways in the generation of human horizontal OKN and an evolutionary takeover of the higher levels of the cortex. At the very least, the differences in the responses to plaids between cats and humans are consistent with the hypothesis that the involvement of the subcortical pathway is less in humans than in cats.

The role of pursuit in interpreting the response to plaids

One difficulty in assessing the present results is that we might not be looking at OKN at all but, instead, smooth pursuit. Or at least the pursuit system, with its powerful closed-loop feedback, might be contributing to the eye movement response. It is difficult to argue this point because the pursuit system and the so-called fast build-up subsystem of OKN might not actually be different. Another way of stating our conclusion (that with evolution, the higher levels of the cortex come to dominate the control of OKN) might be with evolution, the pursuit system comes to dominate OKN. The differences between the cat's and man's response to plaids parallel the difference between those species' ability to pursue (cat: Evinger & Fuchs, 1978; human: Pola & Wyatt, 1985) and to demonstrate the fast build-up phase of OKN (cat: Maioli & Precht, 1984; human: Collewijn, 1985).

Future uses of this technique

In young normal infants and patients who had various eye disorders (such as strabismus or cataracts) during early infancy, large simple patterns elicit vigorous OKN to nasalward stimulus motion but little or no OKN to temporalward stimulus motion (e.g. Lewis et al., 1989; Reed et al., 1991). The usual explanation for this asymmetry is that OKN in these populations is dominated by subcortical pathways which favor nasalward motion (e.g. Hoffmann, 1989; Lewis et al., 1989; but see Norcia et al., 1991a,b). Testing the OKN of these populations with plaids provides an opportunity to test that hypothesis. One previous study measured optokinetic responses to plaids in normal infants but included only binocular tests, so the subcortical contribution to OKN could not be evaluated (Manny & Fern, 1990). Our relatively fast and noninvasive procedure now opens the way to a series of investigations using plaids to distinguish cortical and subcortical influences on the optokinetic generator. Caution must be exercised, however, in interpreting any nasal/temporal asymmetry because it could have a source other

than the primarily crossed nature of the direct retinal projections to the brain stem. For example, studies using evoked potentials have revealed asymmetries in the cortical response to temporalward vs. nasalward motion in strabismics and in normal young infants (Norcia et al., 1991a,b). Independent measures of cortical symmetry are needed to interpret any asymmetry detected in the OKN response to plaids of such subjects. Interestingly, the response to plaids may aid even in assessing the relative contributions from both the (asymmetric) direct retinal pathways and an asymmetrical cortex. Smith and Harris (1991) show that an arithmetic weighting system can be used to model the inputs.

Regardless of the relevance to other populations, the implications of the present study are interesting. Had we found a nasal/temporal asymmetry in the response to plaids, this would have implied an influence of the direct subcortical pathway: in normal human adults, the cortex responds symmetrically to nasalward and temporalward motion (Norcia et al., 1991b). However, we found no such nasal/temporal asymmetries, a finding which might suggest little or no influence of the direct subcortical pathway in the generation of OKN in normal human adults.

Acknowledgments

Supported by NIH EY03475 to D. Maurer and NSERC (Canada) OGP0046271 to L.R. Harris. We would like to thank our subjects for their cooperation and Ian Howard for the infrared recording device. Credit for the original idea for using plaids as an OKN stimulus is due to Andy T. Smith of the University of Wales College of Cardiff. We would also like to thank The Institute for Space and Terrestrial Science (ISTS) for their support.

References

- AAS, J.E. (1989). Subcortical projections to the pontine nuclei in the cat. *Journal of Comparative Neurology* **282**, 331-354.
- ADELSON, E.H. & MOVSHON, J.A. (1982). Phenomenal coherence of moving visual patterns. *Nature* **300**, 523-525.
- BJAALIE, J.G. & BRODAL, P. (1989). Visual pathways to the cerebellum — segregation in the pontine nuclei of terminal fields from different visual cortical areas in the cat. *Neuroscience* **29**, 95-107.
- BLAKEMORE, C.B. & HILLMAN, P. (1977). An attempt to assess the effects of monocular deprivation and strabismus on synaptic efficiency in the kitten's visual cortex. *Experimental Brain Research* **30**, 187-202.
- CARPENTER, R.H.S. (1988). *Movements of the Eyes*. London: Pion.
- COLLEWIJN, H. (1985). Integration of adaptive changes of the optokinetic reflex, pursuit and the vestibulo-ocular reflex. In *Adaptive Mechanisms in Gaze Control*, ed. BERTHOZ, A. & MELVILL JONES, G., pp. 51-69. New York: Elsevier.
- CYNADER, M. & HARRIS, L. (1980). Eye-movement in strabismic cats. *Nature* **286**, 64-65.
- EVINGER, C. & FUCHS, A.F. (1978). Saccadic, smooth pursuit and optokinetic eye movements in the trained cat. *Journal of Physiology* **285**, 209-229.
- FERRERA, V.P. & WILSON, H.R. (1990). Perceived direction of moving two-dimensional patterns. *Vision Research* **30**, 273-287.
- GIZZI, M.S., KATZ, E., SCHUMER, R.A. & MOVSHON, J.A. (1990). Selectivity for orientation and direction of motion of single neurons in cat striate and extrastriate visual cortex. *Journal of Neurophysiology* **63**, 1529-1543.
- GRASSE, K.L. & CYNADER, M.S. (1984). Electrophysiology of lateral and dorsal terminal nuclei of the cat accessory optic system. *Journal of Neurophysiology* **51**, 276-293.
- GRASSE, K.L. & CYNADER, M. (1991). The accessory optic system in frontal-eyed animals. In *Vision and Visual Dysfunction. Vol. 4. The Neural Basis of Visual Function*, ed. LEVENTHAL, A.G. pp. 111-139. Boca Raton: CRC Press.

- HARRIS, L.R., LEPORE, F., GUILLEMOT, J.-P. & CYNADER, M. (1980). Abolition of optokinetic nystagmus in the cat. *Science* **210**, 91–92.
- HARRIS, L.R., LEWIS, T.L. & MAURER, D. (1991). Plaids used to evaluate cortical and subcortical involvement in human optokinetic nystagmus (OKN). *Investigative Ophthalmology and Visual Science* (Suppl.) **32**, 1021.
- HARRIS, L.R. & SMITH, A.T. (1990). Plaids used to distinguish direct retinal and cortical contributions to horizontal optokinetic nystagmus. *Investigative Ophthalmology and Visual Science* (Suppl.) **31**, 591.
- HOFFMANN, K.-P. (1983). Control of the optokinetic reflex by the nucleus of the optic tract in the cat. In *Spatially Oriented Behavior*, ed. HEIN, A. & JEANNEROD, M., pp. 135–153. New York: Springer Verlag.
- HOFFMANN, K.-P. (1989). Control of the optokinetic reflex by the nucleus of the optic tract in primates. *Progress in Brain Research* **80**, 173–182.
- HOFFMANN, K.-P. & DISTLER, C. (1986). The role of direction selective cells in the nucleus of the optic tract of cat and monkey during optokinetic nystagmus. In *Adaptive Processes in Visual and Oculomotor Systems*, ed. KELLER, E.L. & ZEE, D.S., pp. 261–266. Oxford: Pergamon.
- HOFFMANN, K.-P., MADER, W., DISTLER, C. & ERICKSON, R.G. (1988). Physiological and anatomical identification of the nucleus of the optic tract and dorsal terminal nucleus of the accessory optic tract in monkeys. *Experimental Brain Research* **69**, 635–644.
- HOFFMANN, K.-P. & SCHOPPMANN, A. (1975). Retinal input to direction selective cells in the nucleus tractus opticus of the cat. *Brain Research* **99**, 359–366.
- HOFFMANN, K.-P. & SCHOPPMANN, A. (1981). A quantitative analysis of the direction-specific response of neurones in the cat's nucleus of the optic tract. *Experimental Brain Research* **42**, 146–157.
- HOWARD, I.P. & OHMI, M. (1984). The efficiency of the central and peripheral retina in driving human optokinetic nystagmus. *Vision Research* **24**, 969–976.
- KATO, I., HARADA, K., HASEGAWA, T., IGARASHI, T., KOIKE, Y. & KAWASAKI, T. (1986). Role of the nucleus of the optic tract in monkeys in relation to optokinetic nystagmus. *Brain Research* **364**, 12–22.
- LEWIS, T.L., MAURER, D. & BRENT, H.P. (1989). Optokinetic nystagmus in normal and visually deprived children: Implications for cortical development. *Canadian Journal of Psychology* **43**, 121–140.
- MAIOLI, C. & PRECHT, W. (1984). The horizontal optokinetic nystagmus in the cat. *Experimental Brain Research* **55**, 494–506.
- MANNY, R.E. & FERN, K.D. (1990). Motion coherence in infants. *Vision Research* **30**, 1319–1329.
- MONTAROLO, P.G., PRECHT, W. & STRATA, P. (1981). Functional-organization of the mechanisms subserving the optokinetic nystagmus in the cat. *Neuroscience* **6**, 231–246.
- MOVSHON, J.A., ADELSON, E.H., GIZZI, M.S. & NEWSOME, W.T. (1986). The analysis of moving visual patterns. *Experimental Brain Research* (Suppl.), **11**, 117–152.
- MUSTARI, M.J. & FUCHS, A.F. (1989). Discharge patterns of neurons in the pretectal nucleus of the optic tract (NOT) in the behaving primate. *Journal of Neurophysiology* **64**, 77–90.
- MUSTARI, M.J. & WALLMAN, J. (1988). Response properties of dorso-lateral pontine units during smooth pursuit in the rhesus macaque. *Journal of Neurophysiology* **60**, 664–686.
- NORCIA, A.M., GARCIA, H., HUMPHRY, R., HOLMES, A., HAMER, R.D. & OREL-DIXLER, D. (1991a). Anomalous motion VEPs in infants and in infantile esotropia. *Investigative Ophthalmology and Visual Science* **32**, 436–439.
- NORCIA, A.M., JAMPOLSKY, A., HAMER, R.D. & OREL-DIXLER, D. (1991b). Plasticity of human motion processing following strabismus surgery. *Investigative Ophthalmology and Visual Science* (Suppl.), **32**, 1044.
- POLA, J. & WYATT, H.J. (1985). Active and passive smooth movements: Effects of stimulus size and location. *Vision Research* **25**, 1063–1076.
- REED, M.J., STEINBACH, M.J., ANSTIS, S.M., GALLIE, B., SMITH, D. & KRAFT, S. (1991). The development of optokinetic nystagmus in strabismic and monocularly enucleated subjects. *Behavioral Brain Research* **396**, 31–42.
- SCHIFF, D., RAPHAN, T. & COHEN, B. (1988). Nystagmus induced by stimulation of the nucleus of the optic tract in the monkey. *Experimental Brain Research* **70**, 1–14.
- SIMPSON, J.I. (1984). The accessory optic system. *Annual Review of Neuroscience* **7**, 13–41.
- SIMPSON, W.A. & SWANSTON, M.T. (1991). Depth-coded motion signals in plaid perception and optokinetic nystagmus. *Experimental Brain Research* **86**, 447–450.
- SMITH, A.T. & HARRIS, L.R. (1991). Use of plaid patterns to distinguish the corticofugal and direct retinal inputs to the brain-stem optokinetic nystagmus generator. *Experimental Brain Research* **86**, 324–332.
- STRONG, N.P., MALACH, R., LEE, P. & VAN SLUYTERS, R.C. (1984). Horizontal optokinetic nystagmus in the cat: Recovery from cortical lesions. *Developmental Brain Research* **13**, 179–192.
- TUSA, R.J. & ZEE, D.S. (1989). Cerebral control of smooth pursuit and optokinetic nystagmus. *Current Neurology and Ophthalmology* **2**, 115–146.
- VAN DEN BERG, A.V. & COLLEWIJN, H. (1988). Directional asymmetries of human optokinetic nystagmus. *Experimental Brain Research* **70**, 597–604.
- WELLS, G.R., YEO, C.H. & HARDIMAN, M.J. (1989). Visual projections to the pontine nuclei in the rabbit – orthograde and retrograde tracing studies with WGA-HRP. *Journal of Comparative Neurology* **279**, 629–652.
- WOOD, G.C., SPEAR, P.D. & BRAUN, J.J. (1973). Direction-specific deficits in horizontal optokinetic nystagmus following removal of visual cortex in the cat. *Brain Research* **60**, 231–237.
- ZEE, D.S., TUSA, R.J., HERDMAN, S.J., BUTLER, P.H. & GUCER, G. (1987). Effects of occipital lobectomy upon eye movements in primate. *Journal of Neurophysiology* **58**, 883–907.

Appendix

What happens to plaids on the retina when the eyes move?

The relative motions of the grating components determine the coherent direction of movement of a plaid. Since the components move in different directions and, for the plaids considered in this paper, at different speeds, any eye movement will affect the retinal velocity of each component differently. This means that the direction and velocity of a coherent pattern constructed from these altered components on the retina will be different from that presented on the screen.

Fig. 10 shows graphically the effect of eye movements. The plaid chosen for Fig. 10 is a type A plaid with a coherent direction of 328 deg (see legend to Fig. 2). It was judged as moving straight up when presented monocularly (see Fig. 5A). It is a convenient example conceptually because it evokes no horizontal eye movements (see Fig. 4A) but the geometry is the same for all plaid orientations. Any upward eye drift alters the speed of each of the gratings that make up the plaid by the speed of the component of the added vector in the direction of motion of that grating. It will not alter the direction of a grating's motion (other than in some cases to reverse it), since a one-dimensional grating can only move orthogonal to its orientation. The direction of coherent motion for each plaid that results from these new grating speeds is equivalent to a vector sum between the original coherent direction and the added vector. Speeds of 10.5 and 15.2 deg/s (Fig. 10B) shift the coherent direction from 328 to 297 deg and 271 deg, respectively. This compares to components at 28 deg (a2) and 223 deg (b2) for 10.5 deg/s and 208 deg (a3) and 223 (b3) for 15.2 deg/s. Clearly neither the judgement ("12 o'clock") nor the interpolated direction of eye movements (upward) is determined by the retinal motion but instead from the real motion which the brain must deduce by interpreting the retinal image in the context of knowledge about eye movements.