Use of plaid patterns
to distinguish the corticofugal and direct retinal inputs
to the brainstem optokinetic nystagmus generator

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Summary. We have recorded the direction of optokinetic nystagmus (OKN) elicited by moving plaid patterns in order to dissociate the pathways that mediate horizontal OKN. The plaids used comprised two drifting sinusoidal gratings arranged such that their individual directions of drift were very different from the direction of coherent motion of the overall pattern. The direction of OKN with binocular viewing was close to the mean of the component directions, suggesting a dominant influence of cortical visual neurons that respond to oriented one-dimensional components of the image. But the direction of OKN was consistently shifted slightly towards the direction of motion of the overall pattern, suggesting a secondary influence responsive to pattern direction. OKN recordings obtained during monocular viewing suggest that this secondary influence reflects the direct retinal pathway to the brainstem structures mediating OKN.

Key words: Vision – Optokinetic nystagmus – Eye movements – Plaids – Brainstem – Motion perception – Cat

Introduction

Eye movements, in particular the vestibulo-ocular reflex and its visual counterpart optokinetic nystagmus (OKN), are important for minimizing the blurring of the retinal image that would otherwise be caused by the continual movement of the head and body. These compensatory eye movements normally occur in the direction of image movement, tending to stabilize the image allowing clear vision to continue. OKN may be elicited experimentally by whole-field image movement (which in nature is usually caused by head movement) in the absence of any head movement.

Visual information pertinent to OKN is channelled

through the accessory optic system. In the cat, the nucleus of the optic tract (NOT) has been implicated in the control of horizontal OKN (Hoffman 1982; Collewijn 1975a; Maekawa et al. 1984; Schiff et al. 1988), other nuclei mediating vertical OKN (see Grasse and Cynader 1990; Simpson 1984 for reviews). It is tacitly assumed that movement in any given direction is produced by summing the outputs of these nuclei. Neurons of the right NOT respond preferentially to motion in the rightward direction, those of the left NOT to leftward motion (Hoffmann and Distler 1986; Grasse and Cynader 1984). Direct evidence concerning the relationship between NOT output and OKN is sparse, but electrical stimulation studies (e.g. Collewijn 1975b; Schiff et al. 1988) suggest that each NOT generates eye movements only in the direction to which its neurons are visually responsive.

The NOT receives visual inputs via two quite separate pathways (see Fig. 4). The first is a direct pathway from retinal ganglion cells (Ballas et al. 1981). This predominantly involves W-cells (Hoffmann 1986). The projection is functionally entirely crossed (Hoffmann and Shoppmann 1975; Harris et al. 1980), so that the direct pathways are involved only in nasal stimulus movement (leftward through the right eye, and rightward through the left eye). The other pathway is an indirect input to the NOT from the visual cortex. Relatively little is known of the origins of this indirect cortical pathway or of the nature of the visual information it conveys. In the cat it originates at least partly in the primary (striate) visual cortex (area 17), extrastriate cortex (area 18) and the suprasylvian cortex (Montarolo et al. 1981; Marcotte and Updyke 1982; Herdman et al. 1989; Tusa et al. 1989). Shoppmann (1981) has shown that the direction-sensitive layer V pyramidal cells of areas 17 and 18 are involved and that the projection is binocular. Visual information from the cortex may also influence optokinetic nystagmus via projections onto other brainstem structures (eg. the dorsolateral pontine nuclei: Bjaalie et al. 1989; Mustari et al. 1988)

It has sometimes been considered that the direct reti-

nal pathway is dominant in the generation of OKN and that the corticofugal pathway is secondary. After all, OKN is present in animals with little or no cortex (eg. goldfish: Easter et al. 1975). And in both phylogeny and ontogeny the indirect pathway develops later, supplementing an already functional brainstem circuit (Flandrin et al. 1979; Atkinson 1979). In the cat, OKN persists after ablation of the cerebral cortex (although its effectiveness is impaired: Wood et al. 1973; Ventre 1985). All these observation suggest that OKN is a primitive brainstem controlled reflex to which the cortex contributes only a refining influence. However Hoffmann (1986) has suggested that in higher mammals the cortical pathway may in fact have become the dominant pathway in OKN control, superseding the phylogenetically more ancient direct pathway. Increasing dominance of the cortical influence may be an evolutionary trend, culminating in an almost non-functional direct pathway in man.

We have compared the relative dominance of the direct and corticofugal pathways behaviourally by taking advantage of the fact that these two pathways can be expected to have different kinds of directional selectivity, referred to as pattern direction and component direction selectivity:

"Component directional selectivity corresponds to what previous workers would have termed orientation selectivity with directional selectivity. Neurons showing component direction selectivity respond to the direction of motion of single oriented (1-D) contours presented in isolation, and to the direction of motion of those contours when they form part of a more complex 2-D pattern. Pattern direction selectivity corresponds to what previous workers have termed 'pure' direction selectivity. Neurons showing pattern direction selectivity, like component neurons, respond to the direction of motion of isolated 1-D contours. When those contours are imbedded in a more complex 2-D pattern, however, these neurons respond not to the motion of the contours, but to the motion of the pattern as a whole." (Movshon et al. 1986 p 136).

NOT cells influenced primarily by the direct pathway, being non-oriented (Hoffmann and Shoppmann 1975), should show "pattern" or "pure" direction selectivity. The expected behaviour of NOT cells influenced predominantly by the cortical route depends on the type of cortical neurons involved. If driven by non-oriented cortical neurons, NOT cells should show pattern direction selectivity just as if they were influenced by non-oriented retinal ganglion cells. But any influence of orientation-tuned cortical cells (which in cats form the overwhelming majority of cortical neurons) should be reflected in component direction selectivity in NOT.

The usual stimulus used in OKN experiments is a large, high-contrast pattern of moving dots. Such a stimulus can be expected to drive neurons of both types of directional selectivity whose direction preferences correspond to the direction of motion of the dots. The same is true for most other visual stimuli. In contrast, a plaid formed by adding two or more drifting gratings of different orientations (Adelson and Movshon 1982, see Fig. 1), can be arranged to drive neurons of different direction-selectivity types differently. The plaid illustrated in Fig. 1 has been carefully constructed (see methods) to excite cells with "component" direction selectivity whose preferred directions have a rightward horizontal vector, whilst simultaneously activating cells with "pattern" direction selectivity whose preferred directions have a leftward horizontal vector. The direction of the OKN elicited by this stimulus may thus reveal which type of neuron, and hence which part of the visual system, is driving the eye movements. The cat was used in these studies because it has poor smooth pursuit (Evinger and Fuchs 1978) so that pursuit would not confuse the interpretation of the results.

Methods

Preparation

Two adult female cats were prepared under sterile operating conditions and Saffan anaesthetic (alfaxolone i.v. induction dose 18 mg/kg supplemented with additional doses as required). A preformed scleral search coil (A5632 Cooner Wire Company, Robinson, 1963) was placed under the conjunctiva around the sclera. Head restraining tubes (Kopf) were fixed in dental cement on the top of the skull. The method is described in detail in Harris and Cynader (1981)

Stimuli

The visual stimuli used were plaids formed by the addition of two sine gratings of different orientations (Fig. 1). They were presented on a large-screen X/Y display (HP1310A) and were viewed in an otherwise dark room. The image subtended 48 deg at the viewing distance of 35 cm. The gratings used all had a fixed spatial frequency of 0.5 c/deg. The contrast of each grating was 25%, giving
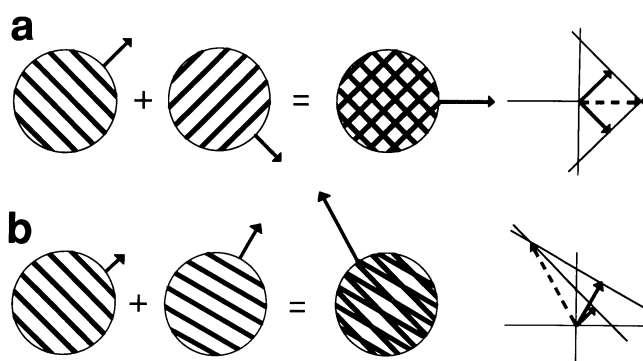
Fig. 1a, b. Type I (a) and type II (b) plaids (nomenclature after Ferrera and Wilson 1990). The direction of coherent motion of any plaid is predictable from the intersection in velocity space of the velocity constraint lines of the two components (see Adelson and Movshon 1982). The direction specified by the intersection of constraints will be referred to in this paper as the "pattern direction", after Adelson and Movshon (1982). For type I plaids, the pattern direction falls within the components (here at +90: in between +45 and +135); for type II plaids the pattern direction falls outside the components (here at −30 where the components are at +30 and +45)

a contrast of 50% for plaids comprising the sum of two such gratings. Grating patterns of these parameters have been shown to stimulate the cat's OKN system adequately (Donaghy 1980).

Using the nomenclature of Ferrera and Wilson (1990), plaids can be divided into two types in which the coherent direction of motion of the whole pattern falls either between (type I: eg. Fig. 1a) or outside (type II: eg. Fig. 1b) the directions of its components. Fig. 1 shows the examples of each type that we used in this study. We will use the following convention to specify direction: 0 = upward, +90 = rightward, −90 = leftward. Figure 1a shows a plaid comprising gratings separated in orientation by 90 degs and both moving at the same speed. The resulting coherent motion is midway between the components and this plaid is therefore type I. Figure 1b shows a plaid with components drifting at +30 deg and +45 deg with drift speeds of 4.5 deg/s and 2.3 deg/s respectively. The resulting coherent motion is at −30 deg with a speed of 9.0 deg/s (see Movshon et al. 1986, for a detailed explanation of how to calculate the direction and speed of pattern motion). The pattern direction is thus well away from that of the components and this is a type II plaid. Note that the horizontal vectors of both components (and of their mean) were rightward whilst that of the overall pattern motion was leftward.

The two plaids illustrated in Fig. 1 represent the basic forms of those used in this study. They could be rotated, mirror imaged or scaled in speed.

Data collection and calibration

During recording sessions the cats were held in a snug-fitting bag (Feline Restraint Inc, Chicago) and their heads were attached to a stereotaxic frame by means of the tubes. The head and body were tilted together 20 deg nose down to bring the plane of the canals into the horizontal (Blanks et al. 1972). Recording sessions were kept as brief as possible to maximize alertness. Patterns were presented continuously for periods of 40 s separated by periods of darkness.

Throughout pattern presentation the vertical and horizontal components of eye position were sampled via D to A converters every 12 ms and stored on disc for off-line analysis. Horizontal calibration was performed by measuring eye movements under conditions where gain is known to be close to unity (Harris 1987). Vertical calibration was calculated from the known ratio of vertical and horizontal signals in the eye coil and confirmed by reference to the oculomotor range.

Data analysis

Estimates of average eye velocity and direction for each stimulus presentation were calculated as follows. For each record a number of periods showing the alternating fast and slow phases characteristic of OKN were identified. The average speed and direction of each of a large number of slow phases was then calculated from the total position change during the slow phase. These data were then averaged across slow phases.

Binocular viewing

Initial experiments used binocular viewing so that all OKN pathways were active.

Binocular viewing: results

*Binocular viewing with single gratings and Type I plaids.* Table 1 summarizes the mean directions and speeds of OKN for type I plaids and single gratings. These results showed no unexpected features. The OKN response to single gratings has been characterized previously and our grating stimuli produced the expected eye movements. The velocity gains, defined as (eye velocity)/(stimulus velocity), were between 0.8 and 0.9 for the gratings for which data are shown. It should be noted, however, that there is a well-known asymmetry in vertical optokinetic nystagmus in which upward moving stimuli are followed more effectively than downward (Evinger and Fuchs 1978; Harris and Cynader 1981); this asymmetry was confirmed. In the type I plaid shown in Fig. 1a, therefore, the two components do not elicit equal responses. This potentially confuses the interpretation of the response to such a plaid. To avoid this complication plaids were chosen whose vertical vector was always upward for both component and pattern directions. Table 1 therefore includes control data only for gratings with an upward vertical vector.

In the case of Type I plaids, OKN direction fell midway between the two component directions. This direction is, of course, coincident both with the mean of the two component directions and with the pattern direction. In view of this, the fact that the OKN falls between the components for type I plaids does not provide a test of our hypothesis that if oriented components drive OKN it will follow the components and that if non-oriented components drive it, it will follow the pattern. It is, however, an important control result since plaid patterns have not to our knowledge previously been used as OKN stimuli.

Binocular viewing with Type II plaids. The result for type II plaids, in which pattern direction and component directions are dissociated, is also summarized in Table 1. The result is clearcut: OKN direction is much closer to component direction than to pattern direction (15.5 ± 1.7 degs). Importantly, however, it does not coin-

Table 1. Speeds and directions of OKN for single gratings and type I and type II plaids. Each number represents the mean for many slow phases measured on at least two occasions from two cats. The number beside each mean is the standard error. Data from leftward stimulus presentations have been mirror imaged and pooled with those from rightward presentations. Direction convention: 0 deg = upward, 90 deg = rightward

Stimulus				OKN	
Stimulus type	Component direction (deg)	Component speed (deg)	Pattern speed (plaids only)	Direction (deg)	Speed (deg/s)
Grating	30	4.5		31.0 ± 1.7	3.9 ± 0.2
Grating	45	2.3		43.0 ± 3.3	2.0 ± 0.3
Type I plaid	+45 and −45	both 2.3	3.2	2.6 ± 3.4	2.6 ± 0.3
Type II paid	+30 and +45	4.5 and 2.3	9.0	15.5 ± 1.7	2.9 ± 0.3
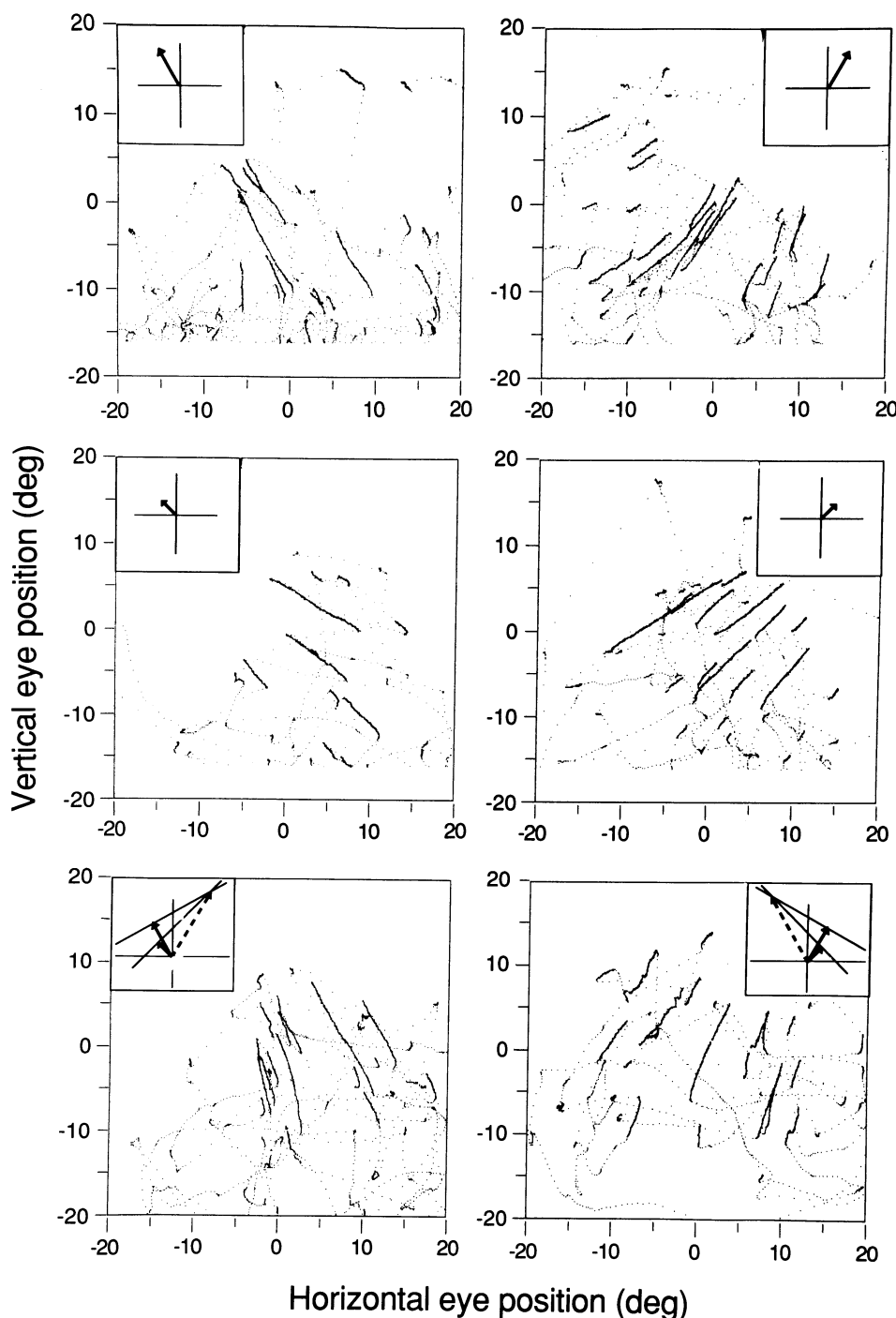
Fig. 2. Two-dimensional plots of eye position during presentation of each of the six stimuli indicated in the insets. Each dot represents the direction of gaze which was sampled at 12 ms intervals. The pronounced streaks (where the dots are close together) indicate the slow phases of OKN: the orientation of the streaks indicates its direction. For the single gratings (top four panels), the orientation closely matches the stimulus (see Table 1). OKN evoked by type II plaids (see Fig. 1b) more closely follows the components rather than the pattern

cide with either of the component directions (30 and 45) or with their mean; indeed it does not fall between the components. Instead it is consistently shifted away from the components and towards the pattern direction. The shift is significant: OKN direction is some 15 degs away from the nearest component or 22.5 deg from their mean (compared with 45 degs away from the pattern direction). Figure 2 illustrates typical OKN responses elicited by the type II plaid described. The responses to the individual sine grating components are also shown for comparison.

We considered the possibility that the coherent drift velocity of the plaid, being greater than the velocity of even the faster component by a factor of two, might be too high to elicit reliable OKN. This is unlikely, since the pattern velocity was only 9.0 degs/s (see Harris et al. 1980; Donaghy 1980). However, if the direct retinal pathway of the OKN system were unable to follow the coherent pattern because of its speed, then clearly only the cortical pathway would be active in the generation of OKN. Although we were careful to choose a plaid whose coherent speed was well within the range of normal OKN

we nonetheless controlled for this possibility in two ways. Firstly, we confirmed that strong OKN could be elicited by a sine grating whose velocity was the same as that of the coherent plaid. Secondly, we repeated the plaid experiment with the component velocities reduced by half, and obtained very similar results in terms of the direction of OKN.

Binocular viewing: discussion

The results suggest that visually-driven OKN is mediated primarily by visual neurons which encode the one-dimensional oriented components of the plaid. This excludes retinal ganglion cells and points to neurons of the primary visual cortex. However, the fact that the OKN does not fall between the components suggests an additional, relatively weak input from non-oriented neurons. Our results are thus in line with the suggestion of Hoffmann (1986) that corticofugal pathways dominate in the production of horizontal optokinetic nystagmus. The results further suggest that the dominant pathways originate at a level in the cortex where neurons are responsive to oriented one-dimensional components of the image.

The secondary input causing a shift towards pattern direction might derive from any of three sources:

(a) non-oriented retinal ganglion cells which respond to the "blobs" in a simple way, i.e. the direct pathway

(b) non-oriented neurons in the same region(s) of cortex as the oriented neurons implicated by our findings

(c) higher-order cortical neurons which have integrated the velocity vectors associated with various one-dimensional components (such as those found in monkey MT; Gizzi et al. 1983). In order to distinguish (a) from (b) and (c), we differentially weighted the direct and indirect pathways by using monocular viewing.

Monocular viewing

The direct and indirect pathways can be given different weightings in the production of optokinetic nystagmus by exploiting the fact that each eye can generate OKN via the direct retinal pathway in only one direction along the horizontal axis (nasally: Hoffmann and Shoppmann 1975). Using the corticofugal pathway, however, OKN in either direction is possible in response to stimuli viewed through either eye. It is thus possible to inactivate the direct pathway completely by the simple expedient of occluding one eye and presenting the stimulus in the direction (temporal) to which the direct pathway from the open eye cannot respond (Harris et al. 1980). OKN elicited in such circumstances must be mediated by the corticofugal pathway. We therefore investigated the involvement of the direct pathway by repeating our experiments using monocular viewing. If the secondary influence responsible for the shift in OKN direction towards the pattern direction reflects the activity of the direct pathway, the shift should be abolished when the direct pathway is inactive. If, on the other hand, it reflects the activity of non-oriented or higher-order cortical neu-

rons, the occlusion of one eye should have little or no effect on the direction of OKN.

Monocular viewing: methods

The methods used were identical to those of the first experiment except that during monocular stimulus presentation, one eye was completely occluded. All conditions were run with each eye occluded, ie. leftward and rightward through the left eye and leftward and rightward through the right eye. This controlled for any other possible ocular asymmetry apart from nasal/temporal difference. No such other asymmetries were noted and so all nasal data and all temporal data have been pooled. Recordings were made from the same two cats in response to the same type II plaids and their grating components alone. For each plaid, left eye, right eye and binocular measures were obtained during the same recording session to allow direct comparison.
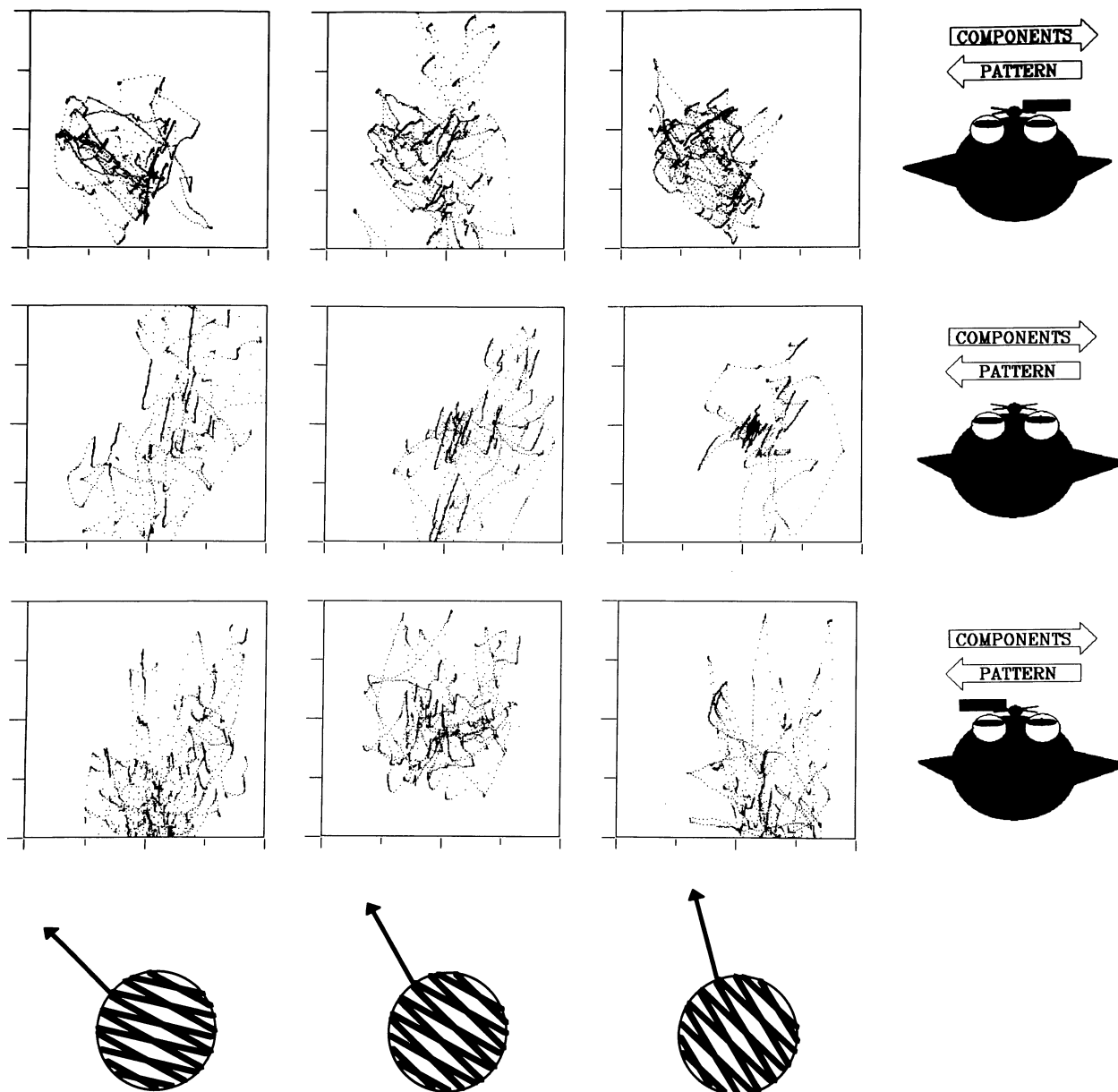
Monocular viewing: results

The top and bottom panels of the central column of Fig. 3 show typical examples of monocular OKN elicited by the plaid used in the binocular experiments. In order to ease interpretation, the stimulus moves in the same direction throughout the diagram (components up and to the right). Viewing is through the left eye in the top row (thus resulting in components moving nasally whilst the pattern moves temporally), binocular in the central row and through the right eye in the bottom row (components temporal, pattern nasal). When the components are nasal, the direction of the evoked OKN falls BETWEEN the direction of the components (36.4 deg in the example shown). That is the shift away from the component directions seen with binocular viewing (central panel and Fig. 2) is now absent. Where component motion is in the temporal direction (pattern nasal), the opposite trend is apparent: the shift away from the component directions towards the pattern direction is now GREATER than for binocular viewing: resulting in almost vertical OKN (6 degs in the example shown). Similar results were obtained for the mirror-image plaid presentations and in both cats. The results are pooled and summarised in Table 2.

Where component motion was in the temporal direction, OKN direction was very close to vertical (bottom

Table 2. Directions of OKN (in degrees) elicited by type II plaids under the conditions illustrated in Fig 3. Averaging and format as for Table 1

Component directions (deg)	15 and 30	30 and 45	45 and 60
Components nasal	20.3 ± 2.4	34.0 ± 3.2	50.1 ± 4.7
Binocular	6.0 ± 1.1	15.5 ± 0.6	28.8 ± 2.2
Components temporal	−7.5 ± 2.1	0.9 ± 2.1	7.2 ± 2.0

Fig. 3. Representative results for monocular viewing of type II plaids. This figure allows two comparisons to be made. Temporal/nasal: The direction of OKN is closer to the components than during binocular presentation (middle row and Fig. 2) when the components are moving nasally (top row). The direction of OKN is further from the components than during binocular presentation when the components are moving temporally (bottom row). Fifteen degree rotations: The central column shows the results obtained with the type II plaid shown in Fig. 1b. The left and right hand columns show the effect of rotating the plaid counterclockwise and clockwise respectively by 15 deg. In all cases the direction of OKN shifts approximately 15 deg also

row, centre panel in Fig. 3). We interpret this as a coincidence: the size of the shift away from the components happens to take OKN to an upward direction. But we wished to eliminate an alternative possibility, that the NOT has shut down leaving only a vertical component to OKN direction. To test this we simply repeated the experiments using a plaid rotated in its entirety through 15 deg, either clockwise or counterclockwise. The left and right columns in Fig. 3 show typical results. Mean pooled results are shown in Table 2. OKN direction changes by about 15 deg in the expected direction for components nasal and binocular viewing conditions. For

monocular viewing with components temporal (bottom row), however, the shift, although in the expected direction was rather smaller than expected (8.4 degs for counterclockwise rotation and 6.3 degs for clockwise).

Discussion

Our results suggest that visually-driven OKN is mediated primarily by visual neurons which encode the one-dimensional oriented components (the gratings) into which a plaid may mathematically be decomposed. In the brain,

such decomposition requires filtering of the image in the orientation domain. It is widely accepted that such filtering is carried out in the cerebral cortex and that one-dimensional oriented components are not represented explicitly at any sub-cortical stage in visual processing. Neurons of the retinal ganglion cell layer and the lateral geniculate nucleus have roughly circular receptive fields that are incapable of responding differentially to differently oriented one-dimensional patterns (although there may be slight orientation biases: e.g. Levick and Thibos 1980; Vidyasagar and Urbas 1982). If OKN broadly follows oriented components, as it does (see Fig. 2 bottom row and Fig. 3 central row), it must be driven primarily by oriented cortical neurons. Retinal ganglion cells (and non-oriented cortical cells) are expected to respond well to plaids, but to the intersections of components (which appear to human observers as "blobs") rather than to the components themselves. Any analysis of direction of motion derived directly from ganglion cells without benefit of the orientation filtering imposed by the cortex must, therefore, be in terms of the motion of these blobs. Such motion is always in the pattern direction i.e. that specified by the intersection of the velocity constraint lines associated with the oriented components (see Adelson and Movshon 1982; Movshon et al. 1986), although it should be noted that to a human observer the perceived pattern direction may differ somewhat from this value (Ferrera and Wilson 1990).

Although the OKN evoked by type II plaids is clearly dominated by the oriented components, the resulting OKN does not fall between the components indicating the presence of an additional influence from another source tending to shift the direction of OKN towards the pattern direction. Our results obtained using monocular viewing suggest strongly that this secondary input to OKN stems from the direct retinal pathway and not from cortical neurons. When viewing is monocular and the horizontal vector of pattern motion is in the temporal direction (so that the direct pathway cannot respond to it), the shift away from the components is abolished and the direction of OKN now lies between the components (top row of Fig. 3 and top row of Table 2). OKN must then be mediated entirely by the dominant cortical pathway involving neurons that respond only to the one-dimensional components of the plaid.

To clarify the argument, the pathways involved are illustrated diagrammatically in Fig. 4 (central panel). When the horizontal vector of pattern motion is in the nasal direction the direct pathway is activated and a strong shift in OKN direction results moving it from 15 to 30 degrees away from the direction of the nearest component (Fig. 4 right hand panel). We interpret this as the result of the cortical pathway activating one NOT whilst the direct pathway simultaneously activates the other. When viewing is binocular the direct pathway from one eye is again active but the shift is reduced in strength, presumably because the cortical input is now stronger since it would receive input from both eyes (as shown in the lefthand panel of Fig. 4).

Our experiments leave open the question of the role of higher cortical areas, such as areas PMLS and VLS in

COMPONENTS / PATTERN   COMPONENTS / PATTERN   COMPONENTS / PATTERN

BINOCULAR   MONOCULAR   MONOCULAR
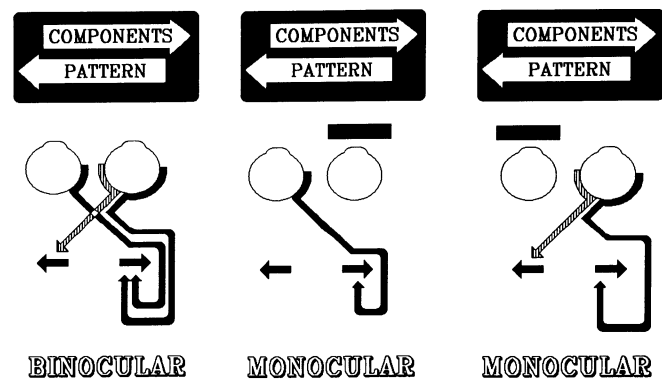
Fig. 4. Diagrammatic representation of the pathways referred to in the text. The left panel shows the cortical and direct retinal pathways that we expect to be active during binocular stimulation. The central panel indicates that with monocular presentation, if the components are nasal, only the indirect pathway should be involved. The right hand panel similarly indicates that, if the components are temporal, both the cortical and the direct pathways should be active, but the cortex, being binocular, will be less stimulated. In addition to those pathways shown, both eyes would also be able to influence the left cortex. In all the illustrated cases these pathways would be symmetrical with those to the right cortex and have been left out of the diagram for clarity

the suprasylvian cortex, that are known to contribute to OKN (Herdman et al. 1989; Tusa et al. 1989; Marcotte and Updyke 1982). Gizzi et al. (1990) have recently shown that neurons in lateral suprasylvian cortex respond to the components of a plaid, just as do those in area 17. Their contribution to OKN therefore cannot be differentiated from that of area 17 neurons by our technique and might be substantial. It is possible that neurons in some other area of extrastriate cortex might respond to pattern direction, as do some neurons in monkey area MT. But if this is the case, our results suggest that the influence of such neurons on OKN direction is very limited since there is no reason why their influence should be altered when the components are temporal with monocular viewing. By the same token, our results suggest that any influence from non-oriented cortical neurons, which are unable to pick out one-dimensional components from a two-dimensional patterns, is slight.

It would be of interest to know whether the results with cats reported here hold for primates, including man. If the involvement of the direct pathway in OKN control is even less than in cats, as Hoffmann (1986) has suggested, then OKN would be expected to follow the components even more closely. However, in man at least, when a drifting plaid is presented in free view there is a strong tendency to make smooth pursuit eye movements in the pattern direction, and careful dissociation of pursuit from OKN would be required in order to test this prediction. In cats, smooth pursuit is extremely limited (Evinger and Fuchs 1978).

For type II plaid stimuli, the dominance of the corticofugal pathway causes an OKN response which, paradoxically, is not optimal for the purpose that OKN is believed to serve: stabilizing the retinal image during head movements. The direction of OKN required to

stabilize the image is always the pattern direction, even where this is very different from the component directions. To appreciate this point consider a plaid painted on a large piece of card which is moved bodily in some direction. Clearly the eyes must move in the direction in which the card is moved in order to maintain a stationary retinal image. But such a stimulus is physically identical to a plaid made from two grating components sliding across each other at appropriate speeds. The presence or absence of slip between the components is simply a matter of interpretation: the interpretation placed on it by the visual cortex. In fact human observers see rigid motion in some circumstances and two gratings sliding across each other in others (Adelson and Movshon 1982). It is, of course, impossible to know which of the two interpretations is perceived by a cat. But the direction of OKN required is independent of which of the two interpretations is used for perception. Thus, in the case of type II plaids the dominance of the corticofugal pathway leads to OKN which is not optimal. In these circumstances OKN would be more effective if mediated by the direct pathway alone. However, in natural images many orientations are usually present and their mean will seldom be far from the pattern direction, so that in practice the involvement of the cortex will seldom reduce significantly the effectiveness of OKN. Any cost that might occasionally be incurred is presumably more than offset by the benefits of cortical involvement.

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