

Up-down asymmetry in human vertical optokinetic nystagmus and afternystagmus: contributions of the central and peripheral retinae

C.M. Murasugi¹ and I.P. Howard^{1, 2}

¹ Department of Psychology and ² Human Performance Laboratory of the Institute for Space and Terrestrial Science, York University, 4700 Keele St., North York, Ontario M3J 1P3, Canada

Summary. The vertical optokinetic nystagmus (OKN) of 10 normal subjects and the optokinetic afternystagmus (OKAN) of 3 subjects were measured with the magnetic search coil technique. In order to assess the relative contributions of various retinal areas to the up-down asymmetry in OKN the central and peripheral visual fields were selectively stimulated in four OKN conditions. In the *full-field* OKN condition the stimulus was a 61°x64° display of moving random-dots. Overall, full-field OKN gains elicited by upward motion were significantly higher than those elicited by downward motion at stimulus velocities between 30 and 70°/s. In the *periphery-only* OKN condition a 3° or 6°-wide vertical band occluded the center of the full-field display. Nine of the 10 subjects displayed OKN in this condition. For 6 subjects, the addition of the 6° band to the full field resulted in an increase in the up-down asymmetry at stimulus velocities above 30°/s. For the other three subjects there was a decline in the gains of both upward and downward OKN when the 3° or 6° band was present; the result was directionally symmetric OKN gains. In the *central-strip* OKN condition only a 6°-wide central vertical strip of moving dots was visible. The gains of central-strip OKN were not significantly different from the full-field responses. A servo controlled centrally-located 10° x 6° moving display was used in the *center-only* OKN condition. In this condition both upward and downward gains were attenuated and there was no up-down asymmetry. OKAN was measured following a 50-s exposure to either the full-field or center-only OKN display. The stimulus velocity was 30°/s. After viewing the full-field display the 3 subjects displayed OKAN with slow phases upward following upward OKN but there was no downward OKAN following downward OKN. In

contrast, there was no consistent directional asymmetry following exposure to the center-only display. The disappearance of the upward preponderance in OKN and OKAN with occlusion of the peripheral retina suggests that the directional asymmetry in vertical OKN exists in the slow OKN system.

Key words: Optokinetic nystagmus – Optokinetic afternystagmus – Directional asymmetries – Central and peripheral retinae

Introduction

Optokinetic nystagmus (OKN) is a series of conjugate eye movements induced by a moving visual field. It is generally believed that the response supplements the vestibular-ocular reflex in stabilizing the image of the visual world during rotations of the head. The slow or tracking phase of the response functions to minimize the retinal slip of the moving image and the fast phase resets the eyes in anticipation of the next slow phase. Following prolonged optokinetic stimulation, the eye movements persist for about 20 s in the dark, a phenomenon known as optokinetic afternystagmus, or OKAN. In this paper, the direction of OKN and OKAN will be specified in terms of the direction of their slow phases.

Gains of upward OKN in the cat and monkey are higher than those of downward OKN (Pasik et al. 1971; Matsuo et al. 1979; Matsuo and Cohen 1984; Grasse and Cynader 1988) and this upward preponderance is greatest at the higher stimulus velocities (Matsuo and Cohen 1984; Grasse and Cynader 1988). These results are consistent with what is known about the response properties of cells in the lateral terminal nucleus (LTN) of the accessory optic system, a primary relay station for

vertical OKN (Simpson et al. 1979). Neurons in the LTN of the cat and monkey have large receptive fields and respond best to large textured stimuli moving in a vertical direction (Grasse and Cynader 1984; Mustari et al. 1988). Single-cell recordings in the LTN of the cat have shown that there are about equal numbers of cells selective to the upward and downward directions (Grasse and Cynader 1984) but that upward-selective cells are tuned to higher velocities than downward-selective cells (Grasse et al. 1984). In the LTN of the monkey, however, the large majority of cells are tuned to the upward direction (Mustari et al. 1988). In both cat and monkey the range of velocity preferences observed in the LTN overlaps extensively with the range of velocities which elicit OKN (Grasse et al. 1984; Mustari et al. 1988).

Investigations of up-down differences in the vertical OKN of normal humans have produced inconsistent results. In earlier studies, some subjects showed an upward and some a downward preference but no overall asymmetry was found (Schor and Levi 1980; Baloh et al. 1983; Hainline et al. 1984; Abadi and Dickinson 1985). These results are difficult to interpret, however, because of methodological concerns. Several investigators (Baloh et al. 1983; Abadi and Dickinson 1985) used electro-oculography (EOG) to measure eye movements, a technique in which an eyelid artifact produces biases in the assessment of vertical eye velocities (Ford 1976; Yee et al. 1985). One study was conducted with the subject's head tilted (Baloh et al. 1983), and subsequent investigators found that the gains of vertical OKN and OKAN, are affected by head position. Matsuo and Cohen (1984) reported that the velocity of upward OKN and OKAN in the monkey is greater when the animal is lying on its side than when it is upright and concluded that inputs from the otoliths influence vertical nystagmus. The very small field size (Schor and Levi 1980) and the use of a single stimulus velocity employed by other investigators (Hainline et al. 1984) also limit the generalizability of their results to other stimulus conditions. However, Van den Berg and Collewijn (1988) recently published a paper in which the precise magnetic search coil method was used to measure the vertical OKN of normal upright subjects. Their results, which appeared in print after we had completed our study, reveal that there is a consistent upward preponderance in human OKN. These investigators used a large display and found the directional asymmetry at stimulus velocities between 9 and 57°/s.

From results of investigations of horizontal

OKN it has been postulated that OKN in primates has two components, a slow mechanism which involves subcortical pathways and a cortically mediated fast mechanism (Cohen et al. 1977; Cohen et al. 1981; Lisberger et al. 1981). The fast system is most prominent in foveate mammals and is thought to be closely related to the smooth pursuit system for flocculectomy disrupts both systems (Zee et al. 1981). The fast system produces the rapid onset of OKN, does not exhibit afternystagmus, and most likely evolved to meet the demands of binocular vision (Cohen et al. 1977; Lisberger et al. 1981; Howard and Gonzalez 1987). The more primitive slow OKN system exists in both foveate and afoveate animals and is characterized by the gradual rise of OKN to constant velocity and by the presence of OKAN (ter Braak 1936; Collewijn 1969). The slow build-up and decay of OKN to and from steady-state velocity is believed to be evidence for an eye velocity storage mechanism, and presumably there are at least four such integrators, one for each of the main directions of movement. Humans, unlike lower mammals, do not usually display a slow build-up of OKN and thus OKAN is the only direct evidence for the existence of the velocity store which exists in the slow OKN system (Cohen et al. 1981). The primary phase of OKAN occurs in the same direction as the preceding OKN, and the secondary phase, when present, has slow phases in the opposite direction (ter Braak 1936; Cohen et al. 1977). In the monkey, OKAN occurs following upward visual stimulation but is less prolonged or absent following downward OKN (Pasik et al. 1971; Matsuo et al. 1979; Matsuo and Cohen 1984). This reveals that there is no velocity storage in the downward direction and provides strong evidence for the view that the up-down asymmetry in monkey OKN is a property of the slow OKN system. The absence of downward OKAN has also been reported for humans (Baloh et al. 1983). However, these investigators used the imprecise EOG technique and tilted their subjects, producing atypical otolith stimulation.

In the present study we first examined whether normal humans tested with their heads upright exhibit an up-down asymmetry in vertical OKN. A large stimulus field and wide range of stimulus velocities were used, and eye movements were measured with the magnetic search coil technique. We found a consistent upward preponderance, as did Van den Berg and Collewijn (1988). Our next goal was to determine whether the up-down asymmetry is a property of the slow or fast OKN system. The response of the slow system was tested both

directly and indirectly. In the indirect method we measured OKN with the central 6° of the retina occluded to reduce the contributions of the smooth pursuit system and the closely related fast OKN. To test for an up-down asymmetry in the slow OKN system we measured OKAN following upward and downward OKN. Finally, we examined whether the up-down asymmetry is present when the moving stimulus is confined to the central visual field, the area most important for driving the fast OKN system (Büttner et al. 1983). Our results support the conclusion that the upward preponderance in human OKN exists in the slow OKN system.

Methods

Subjects

There were seven male and three female subjects, including the authors. They ranged in age between 24 and 60 years, and had no known oculomotor or visual abnormalities except for the need for refractive correction. Seven of the subjects had previously taken part in OKN experiments and three were inexperienced.

Apparatus and eye movement recordings

The OKN display was a white translucent tangent screen in the subject's frontal plane, covered with randomly distributed black dots. The dots subtended 2° of visual angle and had a mean density of 450 dots/m^2 . The angular subtense of the unobstructed part of the screen (described below) was $64^\circ \times 61^\circ$. The screen was the front portion of an endless belt made of white translucent Mylar plastic suspended on four horizontal rollers, one of them driven by a torque motor. The display of black dots could thus be moved upward or downward at various velocities. The screen was illuminated by the light of four tungsten lamps reflected off a white surface. The white part of the display had a mean luminance of 68 cd/m^2 and the entire display had a contrast of 95%. The area surrounding the stimulus was dark.

Vertical and horizontal eye movements were recorded with the magnetic search coil technique (Robinson 1963). The subject was seated on a chair with the head surrounded by two orthogonal pairs of field coils (3 feet diameter). Head position was maintained with a chin rest. The OKN display was just outside the frame of field coils at a viewing distance of 57 cm. The full height of the display was 70° , but the part of the display that was unobstructed by the field coils was 64° -high by 61° -wide. When subjects looked straight ahead 70% of the display was below eye level.

An annular-shaped soft contact lens which contained several turns of a fine wire was placed on the subject's eye after a topical anaesthetic was applied. The lens remained on the eye for approximately 30 min. The eye containing the scleral coil was patched. Myopic subjects wore a regular contact lens in the viewing eye.

For the *center-only* OKN and OKAN conditions, a servo control system (General Scanning Inc. CX660) was used to keep approximately the same retinal area exposed to the moving display. The moving display was viewed through an aperture cut out of a small upright piece of balsawood which was placed 5 cm in front of the subject's eye. The vertical position of the

aperture was controlled by an optical scanner driven by the eye signal. The aperture followed the eye position signal at 100% gain and with less than 2.3° phase lag for input sine-wave frequencies below 0.02 Hz (7° amplitude). For frequencies containing peak velocities in the range of observed slow-phase eye movements, the gain of the aperture position was at least 92% and the phase lag no greater than 9° . A step of 7° reached within 2% of its steady-state velocity in 0.06 s. The subject's head position was maintained with a bite bar when the servo controller was used.

Experimental conditions and procedure

There were four OKN conditions in the study. In the *full-field* condition the stimulus consisted of the $64^\circ \times 61^\circ$ display of moving dots. In the *periphery-only* condition a 6° or 3° -wide black vertical occluder was superimposed on the center of the moving display, and in the *central-strip* condition all but a central 6° -wide vertical strip of the display was covered by black occluders. The occluders were viewed in silhouette and hence were devoid of visible surface features. In the *center-only* condition the moving display was confined within the boundaries of a centrally placed 6° -wide by 10° -high rectangle which moved with the eyes via the servo controller. The four stimulus conditions are illustrated (not to scale) in the insets of Figs. 1 to 4.

The full-field condition was tested first, followed by the periphery-only, central-strip and center-only conditions. All viewing was monocular and each of the two eyes was tested on a separate occasion. The stimulus moved upwards or downwards at velocities of 10, 30, 50 and $70^\circ/\text{s}$, measured at the point opposite the eye. For each stimulus velocity two directions of motion were presented. The order of presentation of velocities and directions was randomized with the constraint that the same velocity was not shown twice in succession.

At the beginning of each OKN session the horizontal and vertical eye-position signals were calibrated by having the subject look at points at known horizontal and vertical eccentricities, including one that was set to the subject's apparent straight ahead. The subject then fixated a centrally-placed laser spot which was the only visible stimulus. To begin each trial the laser spot was removed, the moving screen illuminated and eye-movement recordings initiated. Vertical and horizontal eye-position signals were digitized at 10 ms intervals and recorded on-line by a microcomputer for the trial duration of about 15 s.

Optokinetic afternystagmus was measured following exposure to the full-field and to the center-only displays of moving dots. In both OKAN conditions, eye movements were measured for about one minute in the dark after viewing the display monocularly for 50 s. The stimulus velocity was $30^\circ/\text{s}$. At least two trials were run in each direction. The subjects' spontaneous eye movements in the dark were also recorded.

In all experimental conditions subjects were instructed to view the moving stimulus in a relaxed yet attentive manner, taking care not to pursue an individual feature of the display. These instructions were aimed to elicit "stare" or involuntary nystagmus (ter Braak 1936). In the periphery-only, central-strip and center-only OKN conditions subjects were asked to maintain the horizontal gaze position along the central vertical axis of the band or moving strip while attending to the moving stimuli. The laser spot ensured that subjects were looking at the appropriate place when the stimulus appeared and, as a further precaution, horizontal eye movements were monitored during the trial.

All ten subjects were tested in the full-field and 6° -band conditions and three subjects who exhibited an up-down asym-

metry underwent further testing in the central-strip, center-only and OKAN conditions. The four subjects whose responses were weak with the 6° band were re-examined with the 3° band.

Results

Data analysis

The mean slow-phase velocity of OKN for each 15-s trial was obtained using a computer programme which allowed the operator to reject from the analysis saccades, blinks and other waveforms uncharacteristic of OKN. A similar programme was used to determine the mean velocity of each slow phase of OKAN.

The results from the two eyes were averaged since there was no visible difference between the gains (ratio of slow-phase eye velocity to stimulus velocity) of the left and right eyes.

Full-field OKN

For seven of the ten subjects, OKN gains in response to upward stimulus motion were higher than those in response to downward motion. The mean upward gain was 0.15 higher than the mean downward gain for these subjects. For the other three subjects there was no apparent difference between the gains of the two directions. In Fig. 1 the mean gains of all ten subjects are plotted against stimulus velocity for the two directions. Since both eyes were tested separately, each point is the mean of 20 measurements. Error bars indicate ± 1 SE of the mean.

A two-factor (Stimulus Direction, Stimulus Velocity) analysis of variance (ANOVA) with repeated measures was performed on the OKN gains to test the significance of the directional differences. The main effect of Direction was significant [$F(1, 9)=19.8, P<0.01$], as was that of Velocity [$F(3, 27)=64.1, P<0.001$] and the Direction by Velocity interaction [$F(3, 27)=17.2, P<0.001$]. The effect of Velocity confirmed that OKN gains decreased with stimulus velocity. The presence of the Direction by Velocity interaction indicated that the size of the upward preponderance varied with stimulus velocity, and orthogonal F-tests performed on pairs of means revealed that the upward gain was higher than the downward gain for stimulus velocities greater than 10°/s ($P<0.01$).

Both we and Van den Berg and Collewijn (1988) found an up-down asymmetry in the majority of our subjects: seven of our ten subjects exhibited the effect and Van den Berg and Collewijn reported an upward preponderance in six of their

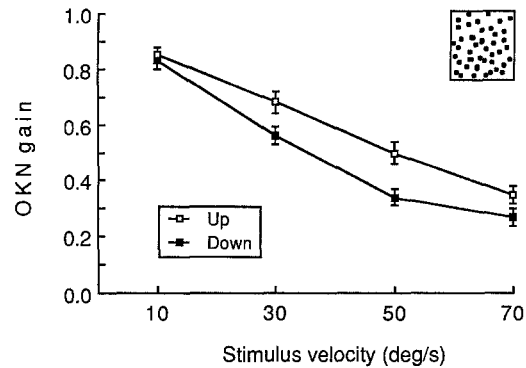


Fig. 1. Mean results of the full-field OKN condition. Mean upward and downward OKN gains of 10 subjects are plotted as a function of stimulus velocity. Each subject was tested twice, once with each eye. The error bars indicate ± 1 SE

seven subjects. Furthermore, the size of the up-down asymmetry we report here is in close agreement with their findings. Van den Berg and Collewijn, however, reported a monocular upward preponderance at a stimulus velocity of 9°/s whereas we found no evidence of a directional asymmetry at a velocity of 10°/s. A close inspection of Van den Berg and Collewijn's monocular data reveals that the standard deviations for downward gains are considerably larger than those for upward gains, especially when the left eye was viewing. In contrast, in their binocular data both the means and standard deviations are similar for the two directions. Perhaps the low mean gains for the downward direction reflects the contribution of one or more subjects who had unusually low downward gains with monocular viewing.

Periphery-only OKN

The data of only nine subjects were analyzed because one subject exhibited very irregular and unanalyzable OKN when either the central 3° or 6° of the display was occluded by the vertical band. He was one of the three subjects who displayed a symmetrical full-field response.

Two clearly distinct patterns of results emerged among the nine subjects in the 6° band condition. For six subjects, including one who showed symmetrical full-field OKN, the mean upward gain was over 85% of the mean full-field response whereas the downward gains declined substantially at the higher stimulus velocities. For the other three subjects, both upward and downward gains declined, resulting in a low-gain and symmetrical response. In fact, for these subjects, both upward and downward gains were lower than the downward gains of the others. These three were experi-

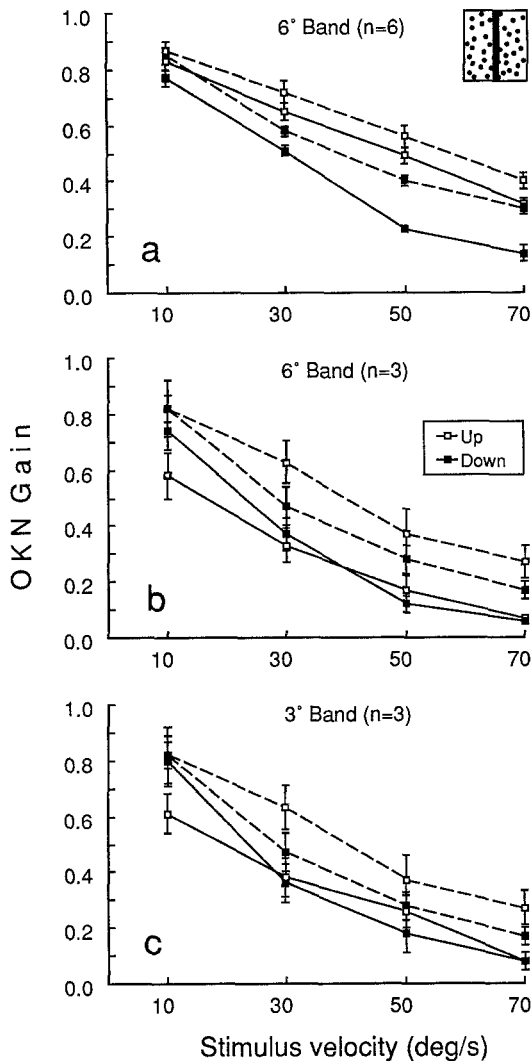


Fig. 2a-c. A comparison of the results of the full-field (dashed lines) and periphery-only (solid lines) OKN conditions. The results of nine subjects are divided into two groups (see text). **a** The OKN gains for the full-field and the 6°-band conditions are plotted as function of stimulus velocity for the two stimulus directions. The data represent the mean of 6 subjects. Error bars indicate ± 1 SE. **b** The OKN gains for the full-field and the 6°-band conditions for the 3 subjects who showed low-gain OKN. Labels and other conventions as in 2a. **c** The OKN gains for the full-field and the 3°-band conditions for the 3 subjects who showed low-gain OKN. Labels and other conventions as in a

enced OKN subjects and also the oldest males of the group.

The results of the 3° and 6° periphery-only conditions are presented in Fig. 2. In this figure the OKN gains for the periphery-only condition (solid lines) are compared with gains for the full-field condition (dashed lines) for the two groups of subjects.

In the three graphs OKN gain is plotted as a function of stimulus velocity for the two stimulus

directions. In Fig. 2a the mean OKN gains of the six subjects who maintained a good upward response are presented. Their data from the 6°-band condition are compared with their full-field gains. Shown in Fig. 2b are the mean results of the three subjects who displayed directionally symmetric OKN gains with the 6° band. Since the gains of these three subjects were depressed overall when the central 6° was occluded, they were retested with a narrower 3° vertical band. There was very little change in their results, as is apparent from Fig. 2c.

To test whether the differences in OKN gains for the two directions varied with stimulus condition, a two-factor (Stimulus Condition, Stimulus Velocity) ANOVA was performed on the differences between the upward and downward gains. Since there were two patterns of results, a separate ANOVA was carried out for each of the two groups of subjects. For the first group of subjects (Fig. 2a), there was a main effect of Stimulus Condition (Full field, 6° Band) which indicated that the mean up-down difference was greater in the presence of the 6° band [$F(1,5)=16.4$, $P<0.05$]. The interaction between Stimulus Condition and Stimulus Velocity approached significance [$F(3,15)=2.6$, $P<0.10$] and according to the results of orthogonal F-tests performed on pairs of group means, the up-down differences were significantly greater ($P<0.001$) with the 6° band at stimulus velocities of 50 and 70°/s. It is clear from Fig. 2a that the increase in the up-down difference with the band is due primarily to the greater decrease in the downward compared with the upward gains. For the second group of subjects (Figs. 2b, 2c) only the effect of Stimulus Condition (Full field, 6° Band, 3° Band) approached significance [$F(2,4)=4.2$, $P<0.11$]. Results of orthogonal F-tests indicated that the mean up-down difference was significantly larger ($P<0.01$) for the full-field condition than when either band was present.

In summary, for six subjects the up-down asymmetry in OKN gain increased with the addition of the 6° band at stimulus velocities of 50 and 70°/s. The increased asymmetry was caused by the pronounced decline in the downward gains at these velocities. For the other three subjects, the up-down difference present with the full-field display disappeared when either a 3° or 6° band was added. Unlike the other six subjects, there was a large attenuation in their upward, as well as, downward OKN gains. In previous experiments in this laboratory we have noticed that subjects vary considerably in the extent to which their peripheral visual fields can drive horizontal OKN. It appears that these three subjects have weak pe-

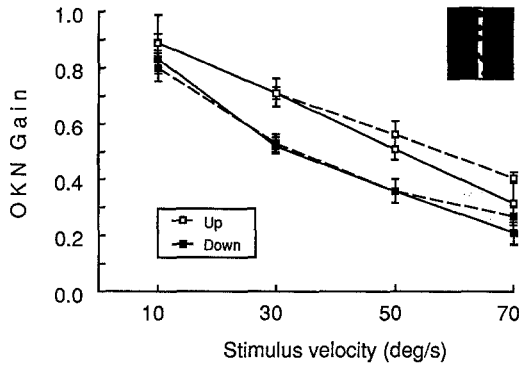


Fig. 3. A comparison between full-field (dashed lines) and 6° central-strip (solid lines) OKN. The OKN gains elicited with the 6° central field and full-field gains are plotted as a function of stimulus velocity for the two directions. The data are the mean of three subjects. Error bars indicate ± 1 SE

ripheral OKN, and with these low gains it is likely that a saturation of the response masked any existing directional differences.

Central-strip OKN

Three subjects who displayed an upward preponderance with the full-field and periphery-only displays were tested in this condition. One of the subjects had shown low gain upward and downward OKN with the central 6 and 3° bands. We found that with stimulation of only the central 6° strip of the moving display, the mean OKN gain was over 90% of the mean full-field gain. The results of the three subjects are shown in Fig. 3. In this figure the OKN gains elicited with the 6° central strip (solid lines) are compared with the full-field gains (dashed lines). For each stimulus condition, the upward and downward gains are plotted as a function of stimulus velocity.

An ANOVA performed on the up-down differences in gain between the full-field and central-strip conditions revealed no main effect of Stimulus Condition, nor an interaction of Condition with Velocity. Thus, the OKN gains elicited by the central 6° of the visual field were not statistically different from the gains elicited by the full field.

Center-only OKN

Two of the three subjects displayed a directional asymmetry, but in opposite directions. Overall, the upward preponderance in OKN gain disappeared when the stimulus was confined to the central retina. In addition, compared with the full-field results there was a large overall decrement in OKN gains at all velocities tested. The data from the three

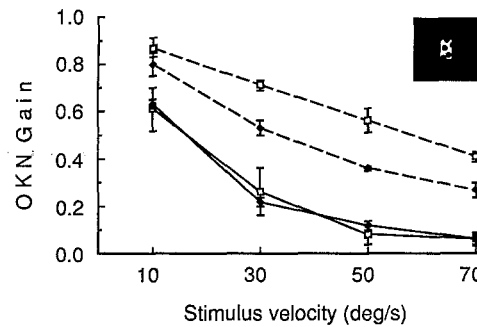


Fig. 4. A comparison between full-field (dashed lines) and center-only OKN. Figure conventions as in Fig. 3

subjects are shown in Fig. 4. The figure conventions are the same as those used in Fig. 3.

Full-field OKAN

We measured the OKAN of the same three subjects who were tested in the central-strip and center-only conditions. They all exhibited an upward preponderance in OKN. The mean OKN gains of the subjects and their standard deviations (SD) measured during the first 15 s of the trials were: up (0.71 ± 0.07), down (0.50 ± 0.05). Following 50 s of OKN stimulation at 30°/s, OKAN varying in duration between 12 and 25 s was recorded. The OKAN velocities of the three subjects in response to upward and downward stimulation are shown individually in Fig. 5. The data were averaged over two trials for WS and MO, and over 4 trials for CM. The velocities of CM's spontaneous vertical eye movements are also shown. The other subjects did not exhibit slow vertical eye movements in the dark.

In Fig. 5 the slow-phase velocities of individual beats of OKAN are averaged across 0.5 s intervals and plotted as a function of the time after stimulus termination. Best-fitting exponential functions were applied to the appropriate OKAN data and their time constants (T_c) are indicated on the graphs.

Subjects MO and WS showed similar results in that OKAN in the upward direction followed upward stimulation and there was no OKAN following downward OKN stimulation. Unlike the others, CM exhibited some upward OKAN following downward OKN. It has been reported previously by Baloh and his colleagues (1983) that some subjects show only secondary OKAN in the upward direction following downward OKN.

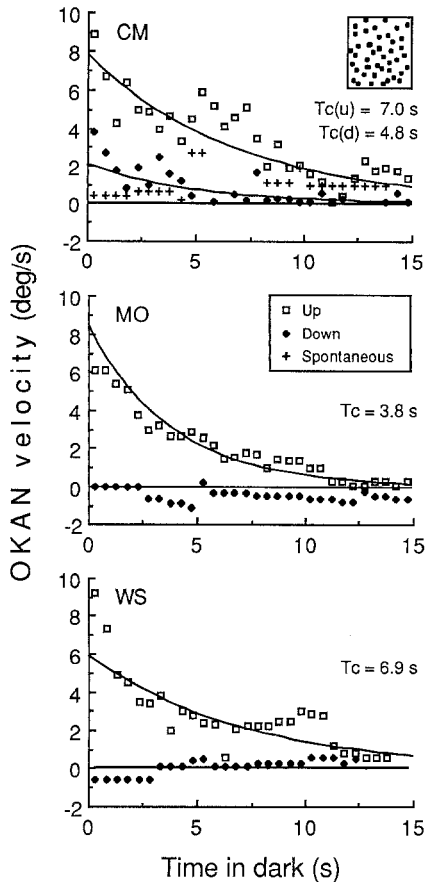


Fig. 5. The OKAN of three subjects following upward and downward full-field stimulation. The mean slow-phase eye velocities of OKAN, averaged across 0.5 s periods, are plotted as a function of time in the dark. Positive values indicate slow-phases in the upward direction, negative values indicate slow-phases downward, and the horizontal line represents zero velocity. Exponential decay curves were fitted to the relevant OKAN data and shown are the individual time constants (T_c) of the functions. The velocities of CM's spontaneous eye movements in the dark are presented

Center-only OKAN

The OKAN following central retinal stimulation generally had lower peak velocities but a similar range of time constants as full-field OKAN. In addition, there was no consistent up-down asymmetry in OKAN, but rather, each subject exhibited a different pattern of asymmetry when the moving stimulus was confined to the central $6 \times 10^\circ$ of the visual field. Furthermore, there was no clear relationship between the peak velocities of OKAN and the gains of the preceding OKN. This can be seen by comparing the means and SDs of the first 15 s of the OKN trials with the peak OKAN velocities: CM displayed the same OKN gains for the two directions (up: 0.21 ± 0.09 ; down: 0.21 ± 0.07) but she had only upward OKAN; MO showed higher OKN gains for downward than for upward motion

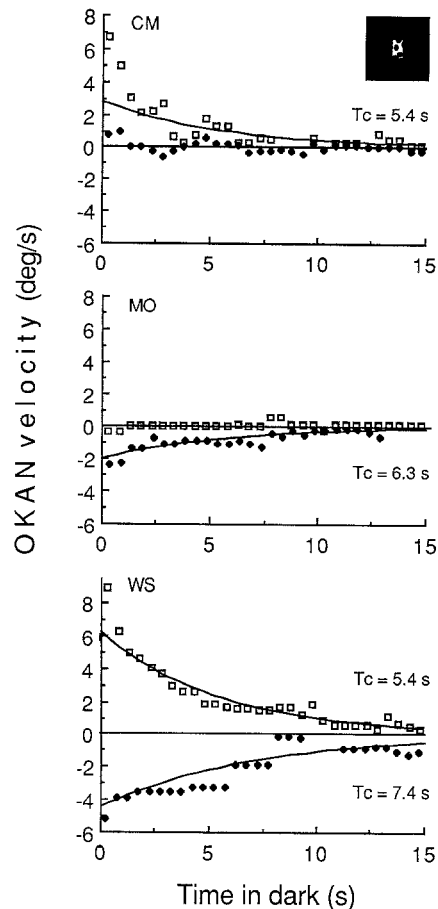


Fig. 6. The OKN of three subjects following center-only OKN. Labels and other other conventions as in Fig. 5

(up: 0.11 ± 0.05 ; down: 0.16 ± 0.05) which is consistent with his OKAN; and WS exhibited much higher upward than downward OKN gains (up: 0.28 ± 0.11 ; down: 0.13 ± 0.05) whereas his upward and downward OKAN responses were similar. These values and the OKAN data presented in Fig. 6 represent the means of two or three trials. In Fig. 6 the slow-phase eye velocities of OKAN are plotted as a function of time for individual subjects.

Discussion

When a full-field moving display is in view, most subjects generate higher OKN gains in response to upward than to downward motion. An identical conclusion was reached by Van den Berg and Collewijn (1988) who also used the magnetic search coil method under similar stimulus conditions. In light of the results of these studies it can be stated with some confidence that humans, like cats and monkeys, exhibit an upward preponderance in vertical OKN. The similar oculomotor behaviour dis-

played by these three species suggests that the neural pathways which control their OKN may share common properties. In the cat the ipsilateral visual cortex mediates the direction selectivity of upward-selective neurons in the LTN whereas downward-selective cells receive their input directly from the contralateral retina (Grasse et al. 1984; Grasse and Cynader 1986). To study the influence of the visual cortex on human vertical OKN it may be worthwhile to examine whether neonates and cortically-damaged patients show direction specific deficits in OKN. The results of the only known developmental study on vertical OKN (Hainline et al. 1984) indicated that infants up to four months of age have higher upward than downward gains whereas older infants and adults show directionally symmetric OKN. The stimulus velocity was $7^\circ/s$. It would be interesting to compare infants' vertical OKN with that of adults at higher velocities where adults exhibit an upward preponderance.

We compared the relative contributions of the central and peripheral retinae to the up-down asymmetry in an attempt to ascertain which of the two subsystems of OKN was responsible for the upward preponderance in vertical OKN. Our results suggest that the asymmetry is a property of the slow OKN system. By occluding all but the central $6 \times 10^\circ$ of the retina we sought to preferentially stimulate the fast OKN system and the related smooth pursuit system, both of which rely on the central retina for their optimum response (Winterson and Steinman 1978; Büttner et al. 1983; Collewijn and Tamminga 1986). It is likely, however, that the slow, as well as the fast OKN system responds to stimulation of the central visual field. Nonetheless, under this stimulus condition we found that both upward and downward OKN gains dropped to less than half of their full-field values, and the up-down asymmetry disappeared. The consistent upward preponderance found in OKAN following full-field stimulation also disappeared following central-field stimulation. The attenuation of the overall OKN and OKAN gains found with peripheral-field occlusion could be the result of the reduced area of stimulation, of inhibitory effects of the proximal horizontal edges of the small display, or to the retinal location of the stimulus. We cannot distinguish between these possibilities on the basis of the present results. Other investigators, however, have reported similar decrements in horizontal OKN gains when comparable stimuli were used (van Die and Collewijn 1982). Our main finding, that the upward preponderance is absent when only the central retina is stimulated, is evidence that the fast OKN is not the main source of the up-down asymmetry in vertical

OKN. It is known that there are no consistent directional asymmetries in smooth pursuit (Baloh et al. 1986). However, stimulation of a narrow strip of the retina along the vertical meridian appears to be sufficient for eliciting an upward preponderance in OKN.

In a complementary stimulus condition, we occluded the central visual field in an attempt to reduce the input to the fast OKN system. Parts of the upper and lower peripheries were also occluded by the vertical band. We found that when only the peripheral visual field was available to drive OKN, downward OKN was considerably attenuated at higher stimulus velocities in all subjects but the upward response was preserved in the majority of subjects. Therefore, generally speaking, the peripheral retina is more effective at eliciting upward than downward OKN. There is additional evidence that the slow OKN system contributes more to upward than to downward OKN. When both central and peripheral visual fields are stimulated OKAN is present following upward but not downward OKN, indicating that velocity storage is reduced or absent for the downward direction even though downward OKN exists. This conclusion is, however, complicated by the fact that when the moving stimulus is confined to the central field, in some subjects there is OKAN with slow phases downwards. One possible explanation for this result is that the afternystagmus elicited by central-field stimulation is not optokinetic but pursuit afternystagmus, which is known to have lower slow-phase velocities but similar time constants to OKAN (Muratore and Zee 1979). Pursuit afternystagmus would not necessarily exhibit the same directional biases as OKAN.

In frontal-eyed animals such as the cat, monkey and humans there is an up-down asymmetry in vertical OKN whereas monocular horizontal OKN is directionally symmetric (Van den Berg and Collewijn 1988). In contrast, lateral-eyed animals, such as the rabbit, show symmetrical (Dubois and Collewijn 1979) or near-symmetrical vertical OKN (Erickson and Barmack 1980) but exhibit monocular OKN only to stimuli moving from the temporal to the nasal visual field, which is the direction of stimulus motion seen by the leading eye during rotations of the head (ter Braak 1936; Collewijn 1969). We shall argue, as have several previous investigators (Benson and Guedry 1971; Grasse and Cynader 1986; Howard and Gonzalez 1987), that directional asymmetries in OKN of frontal and lateral-eyed animals have evolved in response to the dominant optic flow patterns generated by their forward locomotion through space. In other words, the oculomotor system is largely insensitive

to motion in the direction of the most frequently encountered optic flow. The velocity vectors (otherwise known as optic flow) will be expressed in spatial rather than retinal coordinates. Rotations of the head generate homogeneous optic flow throughout the visual field but translations of the head produce vectors of various speeds and/or directions. In lateral-eyed animals the predominant vectors accompanying forward translations are nasotemporal and their velocities vary according to distance. Thus, images of nearby objects move across the retina at higher velocities than objects further away. Since it is impossible to track motion in all depth planes simultaneously, and since lateral-eyed animals lack foveae and stereopsis which would enable them to selectively track a single depth plane, the oculomotor systems of these animals developed a direction-selective response to horizontal motion. Lateral-eyed animals cope with the problem of motion parallax by being largely insensitive to motion in the nasotemporal direction, which is the predominant direction of optic flow during forward locomotion. Humans, on the other hand, have foveae and stereopsis to deal with the problem of motion parallax (Howard and Gonzalez 1987). Stereopsis, however, cannot serve to stabilize the looming, or centrifugal, optic flow pattern which occurs when frontal-eyed animals move forward while looking straight ahead. Probably for this reason frontal-eyed animals developed an upward preponderance in OKN to dampen the influence of the prominent downward optic flow which is present in the lower visual field, the part of the field which contains the greater richness of visual information and the part to which the oculomotor system, horizontal at least, is most sensitive (Murasugi and Howard, 1989). Therefore, the lower sensitivity of the OKN system to downward motion in frontal-eyed animals most likely compensates in part for the visual dominance of the lower field (Skrandies 1987) and allows for better stabilization of the visual field during forward locomotion.

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