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The development of symmetrical OKN in infants: quantification based on OKN acuity for nasalward versus temporalward motion

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Abstract

We quantified OKN asymmetry in 140 normal infants, 3–24 months old, by varying spatial frequency to determine OKN acuity for temporal-to-nasal (T-N) versus nasal-to-temporal (N-T) motion. At all ages, OKN acuity was asymmetrical (better for T-N than for N-T motion) but the size of the asymmetry decreased from 3.2 to 0.7 octaves between 3–24 months, primarily because of improvements in OKN acuity for N-T motion. The results suggest that immaturities in the cortical pathways involved in OKN persist until at least 2 years of age. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Optokinetic nystagmus (OKN) is a series of reflexive eye movements elicited by a repetitive pattern moving through the visual field. OKN consists of two alternating phases of eye movements: slow phase or pursuit eye movements in the direction of movement, and fast phase or saccadic eye movements in the opposite direction. In visually-normal adult humans, monkeys, and cats, horizontal OKN is symmetrical — the alternating pursuit and saccadic eye movements are similar whether the stimulus moves leftward or rightward and whether subjects look with one eye or both (e.g. Pasik & Pasik, 1964; Braun & Gault, 1969; Lewis, Maurer, Smith & Haslip, 1992). When tested binocularly, even newborn babies, young monkeys, and kittens show symmetrical OKN in response to horizontally moving patterns (van Hof-van Duin, 1978; Atkinson, 1979; Krementizer, Vaughan, Kurtzberg & Dowling, 1979). In contrast, when tested monocularly, all three species show asymmetrical OKN during early infancy: OKN is elicited easily when a pattern moves temporally-to-nasally (T-N) but not when it moves nasally-to-temporally (N-T) (e.g. van Hof-van Duin, 1978; Atkinson, 1979; Lewis et al., 1992). The presence of asymmetrical OKN during early infancy has been attributed to immaturities within the cortex and/or to immaturities in the cortical projections to subcortical areas known to be involved in the mediation of OKN, namely the dorsal terminal nucleus of the accessory optic tract and the nucleus of the optic tract in the pretectum (reviewed in Maurer & Lewis, 1993). Charting the development of symmetrical OKN may be a way of charting the development of the functional integrity of the visual cortex and/or its projections to subcortical centres.

Several authors have attempted to determine when OKN becomes symmetrical in normal human infants. Estimates range from 3 months (Atkinson, 1979; Atkinson & Braddick, 1981; van Hof-van Duin & Mohn, 1984, 1985, 1986; Lewis et al., 1992) to 5–6 months of age (Naegele & Held, 1982, 1983; Roy, Lachapelle & Leporé, 1989). All these studies used wide stripes or large random dots of high contrast to elicit OKN. However, the age at which OKN becomes symmetrical may vary with the visibility of the stimulus (i.e. the size and contrast of the elements).

Only one previous study has examined the effect of the visibility of the stimulus on the asymmetry, and did

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so by using a motion nulling technique. Teller et al. (Teller, Succop & Mar, 1993) presented 2-month-olds with two superimposed gratings, one of which moved temporally-to-nasally (T-N) and the other of which moved nasally-to-temporally (N-T), and varied the relative contrast of the two gratings across trials. Infants needed at least 50% more contrast in the grating with N-T motion than in the grating with T-N motion in order to null T-N eye movements. In fact, some infants still showed predominantly T-N eye movements even when there was no T-N motion (contrast set at 0%) and the contrast for gratings with N-T motion was maximal (100%). Although these data are useful for quantifying the degree of eye-movement asymmetries in 2-month-olds, they provide no information on how the degree of asymmetry changes with age. Moreover, the results are not necessarily relevant for assessing OKN asymmetries since testers made a 'forced-choice judgement of the predominant direction…of the infant's eye movements (left-to-right versus right-to-left) on each trial' (Teller et al., 1993, p. 1861) and thus were not required to score OKN eye movements per se.

The purpose of the present study was to quantify the degree of monocular OKN asymmetry throughout infancy by determining the narrowest stripes that would elicit OKN for T-N versus N-T motion. Four groups of infants (3, 5, 12 and 18 month olds) viewed monocularly an 84 × 84° screen entirely filled with vertical stripes moving horizontally across the field at a velocity of 13 deg/s. We assessed OKN acuity (the narrowest stripes eliciting OKN) for each direction of motion. To create narrower stripes for older infants and to test the generalizability of the findings, new groups of 5, 12 and 24 month olds were tested from twice the distance, thereby reducing field size to 42 × 42° and velocity to 6.5 deg/s. We found that the degree of asymmetry (i.e. the difference in octaves between OKN acuity for T-N versus N-T motion) decreased systematically with age and was the same for groups tested at the two distances.

2. Methods

2.1. Subjects

The subjects consisted of seven groups of infants ($N = 20$ per group), four of which were tested 50 cm from the stimuli (3, 5, 12 and 18 month olds) and three of which-were tested 100 cm from the stimuli (5, 12 and 24 month olds). Table 1 lists the mean age and range for each group. Mothers of potential participants were approached at the maternity wards of two local hospitals and the names of volunteers were kept on file until the baby reached the appropriate age. All babies were healthy and free of any known neurological or ocular abnormality. All weighed at least 2500 g at birth, with gestational ages between 38.0 and 42.0 weeks. An additional 28 infants were excluded from the final sample because of refusal to wear the eye patch (one 24-month-old), failure to complete the test (seven 3-month-olds, two 5-month-olds, two 12-month-olds, three 18-month-olds, and two 24-month-olds), procedural errors (one 5-month-old, one 12-month-old, and one 18-month-old), or because the results from phase 2 of the procedure failed to verify the results from phase 1 of the procedure (one 3-month-old, three 5-month-olds, two 12-month-olds, one 18-month-old, and one 24-month-old — see criteria described under Section 2.4).

2.2. Apparatus

The apparatus was similar to that described previously by Lewis, Maurer and Brent (1990, 1995). Briefly,

Table 1
Agreement between phase 1 and phase 2 in estimates of OKN acuity for T-N motion and N-T motion

Age group (months)	Mean age[a] (range) (weeks)	Testing distance (cm)	n[b]	% Of children for whom the two estimates were within:			
				1 Octave		1/2 Octave	
				T-N	N-T	T-N	N-T
3	13.2 (12.3–13.9)	50	21	100	95	62	52
5	21.3 (20.3–22.0)	50	23	96	88	65	52
12	52.2 (51.3–53.1)	50	22	95	95	77	73
18	78.9 (77.4–80.4)	50	21	100	95	100	76
5	21.3 (20.3–22.0)	100	20	100	100	55	60
12	52.7 (51.3–53.1)	100	20	100	100	60	65
24	104.0 (102.0–105.9)	100	21	95	100	67	62
Overall			148	98	96	69	63

[a] Ages are for the 20 subjects per group in the final sample.

[b] Total number tested before exclusion for poor agreement (see Section 2.4).

it consisted of a 90 × 90 cm (84 × 84° when viewed from 50 cm or 42 × 42° when viewed from 100 cm) glass rear projection screen supported and surrounded by black plywood. Stimuli were swept across the screen by a Kodak Ektagraphic projector fitted with a 38 mm Tamron lens projecting through a rotating front-silvered mirror onto the screen 3.25 m away. The mirror was mounted on a turntable calibrated to sweep the stimulus across the screen during each 7-s trial at a velocity of 13 deg/s when viewed from 50 cm (or 6.5 deg/s when viewed from 100 cm). Shielded peepholes (diameter 1 cm) on either side of the screen permitted a clear view of the child's unoccluded eye while preventing a view of the screen.

2.3. Stimuli

For tests at 50 cm, the stimuli consisted of the projected images of 14 black-and-white vertical square-wave gratings of varying spatial frequency, 14 blank control stimuli, and a heterogeneous collection of coloured toys and storybook characters designed to amuse the child between trials. Spatial frequency varied from.05 to 2.5 c/deg in no more than 1/2 octave steps (an octave is a halving or a doubling of a value). For tests at 100 cm, there were two additional spatial frequencies that were a half octave and 1 octave lower than those used for tests at 50 cm so that spatial frequency varied from 0.05 to 5.0 c/deg. Except for the exclusion of one spatial frequency (0.037 c/deg), the stimuli were identical to those described previously by Lewis, Maurer and Brent (1990, 1995). Briefly, slides with the lower spatial frequencies (< 0.75 c/deg when viewed from 50 cm) were created by photographing square-wave gratings (Intergraphics Precision Photographic Services, Kirkland, WA) onto photographic transparencies and mounting them in 40 × 40 mm glass super-slide mounts. Because of limits on the resolution of film, slides with the higher spatial frequencies were created by photographing square-wave gratings directly onto 40 × 40 mm glass plates (Applied Physics, Toronto, Canada). The blank control stimuli were empty slide mounts which permitted light from the projector bulb to illuminate the screen.

Contrast and space-average luminance were measured using a Tektronix photometer, Model J16, fitted with luminance probes J6523 and J6503, respectively. The contrast was 91% for the gratings photographed onto the transparencies (higher spatial frequencies could not be measured). The space-average luminance was 34.9 cd/m^2 for the transparencies, 39.8 cd/m^2 for the glass plates, and 117 cd/m^2 for the blank control trials. Note that we could not use neutral density filters to equate the space-average luminance of the blank field with that of the stripes because the magnified grain of the filters elicited OKN.

2.4. Procedure

The procedure was explained to the parent(s), who were then asked to give written consent. The child had one eye patched (the right eye for half the children in each group and the left eye for the other half) and was seated on a parent's lap so that the unpatched eye was 50 or 100 cm from the screen. The room lights were extinguished and all ambient light came from the projector. In phase 1, two testers watched the child's unpatched eye through peepholes on either side of the screen, with the primary tester always watching through the peephole closest to the child's unpatched eye. One of four highly-trained testers served as the primary tester for each baby and one of three undergraduate thesis students served as the secondary tester.

At the beginning of each trial, the child's attention was attracted to the centre of the screen by projecting a colourful slide, supplemented when necessary by hand shadows and noises. Then the projector was advanced to present stripes that swept across the screen for 7 s. If both testers saw OKN (at least three consecutive beats, with a beat defined as a short pursuit followed by a saccade in the opposite direction), that width of stripe was scored as a 'pass', providing that the eye was steady on the subsequent blank control — which was always the case. Trials during which the testers saw only one or two beats were scored as 'maybe' and repeated, because we could not be certain whether those beats were true OKN or saccades from the child's scanning of the stripes. If the testers saw no OKN, the trial was repeated until the child had accumulated approximately 35 s of looking time with no OKN. That width of stripe was scored as a 'fail'. Trials on which the testers disagreed were repeated. OKN acuity was defined as the highest spatial frequency that the child passed.

Phase 1 was designed to obtain independent estimates of OKN acuity for each direction of motion (T-N and N-T motion). Half of the children in each group were tested first with T-N motion and half, with N-T motion. Because testers' awareness of the direction of motion and spatial frequency during phase 1 might have biased their estimates of acuity, in phase 2 we eliminated that knowledge and used a subset of spatial frequencies to check the estimates of acuity from phase 1. Eight test stimuli (or fewer if the appropriate stimuli were beyond the range of available sizes) were arranged in a random order amongst colourful slides and blank control stimuli like those used in phase 1. The test stimuli consisted of stripes that were one octave wider, half an octave wider, one octave narrower, and half an octave narrower than the estimates of acuity obtained for each direction of motion in phase 1. The primary tester, who was now unaware of spatial frequency and of direction of motion, decided on each trial whether the stimulus elicited OKN and if not, the approximate amount of looking time with no OKN. The secondary tester presented the stimuli, kept track of the primary tester's observations, and using the same criteria as in phase 1, decided when a child had passed or failed each stripe size for a particular direction of motion.

Subjects were included in the final sample only if the results from phase 2 verified the results from phase 1 for each direction of motion. Specifically, for each direction of motion, the primary tester had to report OKN for the stripe size one octave wider than the acuity obtained in phase 1, report no OKN for the stripe size one octave narrower than the acuity obtained in phase 1, and produce systematic results for the two intervening spatial frequencies. Thus, when the data were arranged in order from widest to narrowest stripes for each direction of motion, acceptable patterns were PPFF, PPPF. or PFFF, where P = pass and F = fail. The first pattern constituted agreement within half an octave of the estimate from phase 1, and the remaining two patterns constituted agreement within one octave. All other patterns were considered invalid and the child's data were excluded from the analyses (see Section 2.1 and Table 1).

3. Data analyses

We used nonparametric statistics because Cochran tests (Kirk, 1982, p. 78) indicated that the assumption of homogeneity of variance was violated for most of the statistical comparisons. We used medians to represent group results because of extreme scores in measurements of acuity for N-T motion (see Fig. 2).

To determine whether OKN acuity was asymmetrical, for each group, we used a one-tailed Wilcoxon test of matched pairs to compare the $\log_2$ acuities for T-N versus N-T motion. We set alpha at 0.01 to reduce the likelihood of type 1 error (Howell, 1987, p. 179). Note that a Wilcoxon test eliminates tied scores from the ranks (Siegel, 1956). However, this biases the results by excluding children who had equal OKN acuity for T-N and N-T motion (i.e. symmetrical OKN acuity). To overcome this problem, we assigned a small positive difference score (i.e. T-N better than N-T) to half the tied scores and a small negative score (i.e. N-T better than T-N) of equal absolute value to the other half. The assigned score was smaller than any real difference score. Thus, each Wilcoxon test contained 20 scores ranking the difference between T-N and N-T acuity for the 20 infants at each age. In cases with an uneven number of tied scores, we did two Wilcoxon tests, one with the extra tied score assigned a small positive score and one with the extra tied score assigned a small negative score. The final probability was the mean of the probabilities from the two Wilcoxon tests (see Lewis & Maurer, 1992, for a similar analysis).

To determine if the degree of asymmetry changes with age, we used a Kruskal–Wallis one-way ANOVA on the difference scores (defined as differences in OKN acuity for T-N versus N-T motion, expressed in octaves) for each testing distance. Following a significant effect, we used one-tailed Mann–Whitney U-tests for post-hoc analyses, with alpha adjusted according to the Ryan (1960) procedure. To determine whether testing distance affects the degree of the asymmetry, we used two-tailed Mann–Whitney U-tests, with alpha set at 0.01, to compare results from tests at 50 and 100 cm in the two age groups tested at both distances (5 and 12 month olds).

4. Results

4.1. Agreement between phase 1 and phase 2

For both T-N and N-T motion, about two-thirds of the acuity estimates from phase 2 were within 1/2 octave of those from phase 1 (see Table 1).

4.2. Is OKN acuity asymmetrical?

Fig. 1 shows the difference in octaves between the acuities for T-N and N-T motion for individual infants tested at 50 cm (panel A) or at 100 cm (panel B). Most difference scores were positive indicating that, at every age, acuity for T-N motion was usually better than acuity for N-T motion. Statistical analyses confirmed that OKN acuity was asymmetrical in every group whether tests were at 50 cm (3-month-olds: $T = 0$, $P < 0.0001$; 5-month-olds: $T = 0$, $P < 0.0001$: 12-month-olds: $T = 0$, $P < 0.0001$; 18-month-olds: $T = 2$, $P < 0.0005$) or at 100 cm (5-month-olds: $T = 0$, $P < 0.0001$; 12-month-olds: $T = 0$, $P < 0.0001$; 24-month-olds: $T = 6$, $P < 0.01$ and $T = 5$, $P < 0.01$). Testing distance did not affect the size of the asymmetry for either of the two ages tested at both distances (5-month-olds: $U = 158$, $P > 0.10$; 12-month-olds: $U = 153$, $P > 0.10$).

4.3. Developmental changes in the size of the asymmetry

The size of the asymmetry decreased with age both for tests at 50 cm ($H = 14.75$, $P < 0.01$) and for tests at 100 cm ($H = 15.21$, $P < 0.001$). For tests at 50 cm, the size of the asymmetry decreased significantly between 3 and 18 months ($U = 81.5$, $P < 0.001$, alpha prime = 0.0017) but not between any of the intervening ages (all Ps greater than alpha prime) (see Fig. 1A). For tests at 100 cm, the size of the asymmetry decreased significantly between 5 and 24 months ($U = 90$, $P = 0.001$, alpha prime = 0.007) and between 12 and 24 months

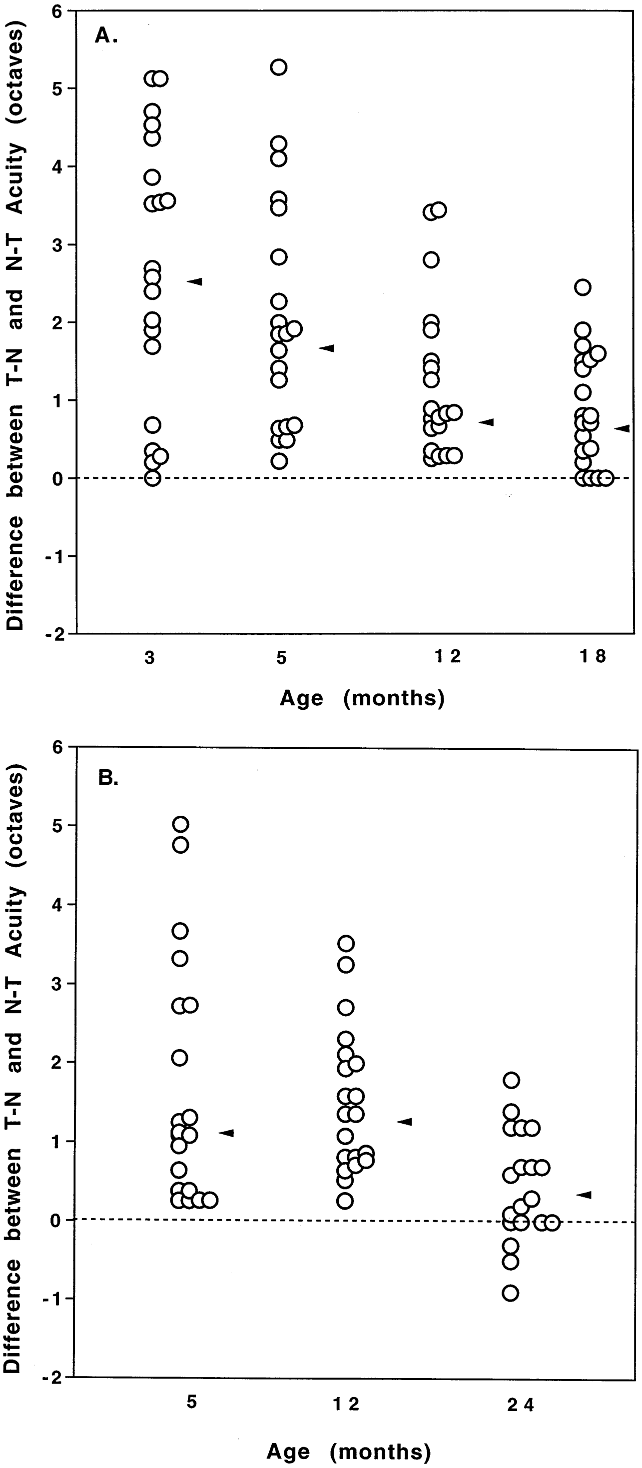

Fig. 1. Distribution of differences in acuity (octaves) for stripes moving temporally-to-nasally (T-N) versus nasally-to-temporally (N-T) for infants in each age group tested from 50 cm (panel A) or from 100 cm (panel B). Positive scores indicate that T-N acuity is better than N-T acuity. Arrows show the median difference score for each group.

($U = 63$, $P = 0.0001$, alpha prime = 0.003), but not between 5 and 12 months ($U = 189$, $P > 0.10$) (see Fig. 1B).

4.4. Developmental changes in T-N and N-T acuity

Fig. 2 shows the distribution of individual acuity scores for each direction of motion in children tested from 50 cm (panel A) and in children tested from 100 cm (panel B). At both testing distances, the results are far more variable for N-T motion than for T-N motion prior to 24 months of age. For the two ages tested at both distances, testing distance did not influence T-N acuity (5-month-olds: $U = 199$, $P > 0.10$; 12-month-olds: $U = 140$, $P = 0.10$) or N-T acuity (5-month-olds: $U = 173$, $P > 0.10$; 12-month-olds: $U = 184$, $P > 0.10$). The median acuities, shown by the arrows in Fig. 2, are replotted for clarity in Fig. 3. As is obvious in Fig. 3, acuity for N-T motion improved more with age than

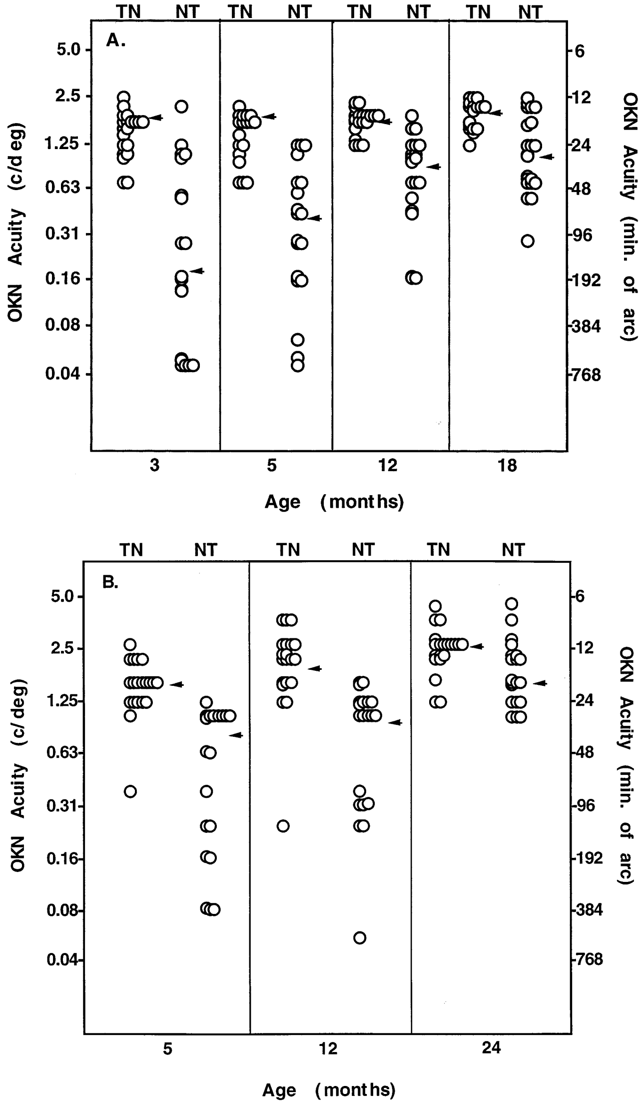

Fig. 2. Distribution of individual OKN acuity scores for stripes moving temporally-to-nasally (T-N) and nasally-to-temporally (N-T) for infants in each age group tested from 50 cm (panel A) or from 100 cm (panel B). Acuity scores are plotted in c/deg along the left axis and in minutes of arc along the right axis. Arrows show the median OKN acuity for each direction of motion.

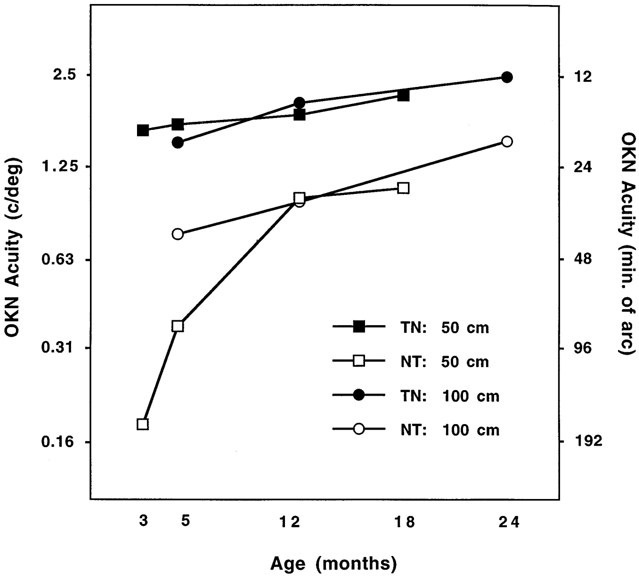

Fig. 3. Median OKN acuity as a function of age for stripes moving temporally-to-nasally (filled symbols) and nasally-to-temporally (open symbols) at a testing distance of 50 cm (squares) or 100 cm (circles). Acuity is plotted in c/deg along the left axis and in minutes of arc along the right axis.

did acuity for T-N motion. Thus, reductions in the size of the asymmetry with age occurred primarily because of changes in acuity for N-T motion.

5. Discussion

5.1. Effects of testing distance

Three groups of infants were tested from 100 cm rather than from 50 cm. This change in testing distance meant that the size of the field was reduced from 84 × 84° to 42 × 42°, stimulus velocity was reduced from 13 to 6.5 deg/s, and the temporal frequency of each spatial frequency was halved. The combination of these changes had no effect on the size of the asymmetry or on OKN acuity for either direction of motion in 5- and 12-month-olds who were tested at both distances. Similar changes would be expected to have no effect on the OKN of normal adults. First, decreasing field size to 20° has no effect on the gain of OKN (Abadi & Pascal, 1991). Second, for a 45° field (the largest tested), OKN gain remains high for stimulus velocities ranging from 3 to 24 deg/s, providing that temporal frequency does not exceed 24 Hz (Schor & Narayan, 1981) (in our study, the temporal frequencies for the spatial frequency immediately below threshold were well below 24 Hz for each direction of motion at all ages). Finally, although normal adults have not been tested, the size of the asymmetry in the good eye of strabismic amblyopes is unaffected by changes in temporal frequency between 3 and 24 Hz. In contrast, for the affected eye of adult strabismic amblyopes, reducing field size from 150 to 45° or increasing temporal frequency from 3 to 24 Hz systematically increases the size of the asymmetry (Schor & Levi, 1980). Thus, changes in temporal frequency and field size appear to affect strabismic amblyopes more than normal infants or adults.

5.2. Developmental changes in the size of the asymmetry

The size of the OKN asymmetry decreased significantly with age, both for tests at 50 cm and for tests at 100 cm. Only at 24 months of age had OKN asymmetry decreased to a trivially small size. Fig. 3 indicates that the size of the asymmetry declines between 3 and 24 months of age because OKN acuity improves more rapidly for N-T motion than for T-N motion. Previous studies reported that OKN becomes symmetrical much earlier — between 3 and 5-6 months of age (Atkinson, 1979; Atkinson & Braddick, 1981; Naegele & Held, 1982, 1983; van Hof-van Duin & Mohn, 1984, 1985, 1986; Roy et al., 1989; Lewis et al., 1992). The discrepancy is likely caused by the fact that all previous studies assessed the development of symmetrical OKN only with large, high-contrast patterns and did not measure responses at threshold.

Developmental changes in OKN acuity and in the size of the asymmetry probably reflect changes in the pathways involved in OKN, rather than changes in motivation or in the size of the visual field. First, OKN is a reflexive response that is not likely to be affected by developmental changes in attention or motivation. Second, such changes cannot account for a greater improvement with age in acuity for N–T motion than for T-N motion. Third, postnatal changes in peripheral vision are unlikely to affect measurements of OKN because, even at birth, the visual field extends out to at least 30 deg for large, high-contrast stimuli (reviewed in Maurer & Lewis, 1998). In adults, OKN is driven mainly by the central 10–20° of the stimulus, although more peripheral parts do make some contribution (Howard & Ohmi, 1984; van Die & Collewijn, 1986; Abadi & Pascal, 1991; Abadai, Howard, Ohmi, Howard, Lee & Wright, 1994; Abadai & Pantazidou, 1997). For example, the gain of OKN elicited by a full-field stimulus is not altered by occluding all but the central 20° but *is* lowered greatly by occluding only the central 20° (Abadi & Pascal, 1991). Moreover, when the motion of the central 20° is in a direction opposite to that of the surround, the direction of OKN matches that of the central patch (Abadi & Pascal, 1991).

There are two major hypotheses about the neural basis of the OKN asymmetry observed in early infancy. Norcia and colleagues (Norcia, Garcia, Humphry, Holmes, Hamer & Orel-Bixler, 1991) hypothesize that OKN is asymmetrical during early infancy because the cortical response to motion is asymmetrical. When infant monkeys and humans monocularly view a grating oscillating horizontally, the visually evoked potential shows a prominent first harmonic component, implying an asymmetry of cortical responses to the two directions of motion (Norcia et al., 1991; Braddick, Mercuri, Atkinson & Wattem-Bell, 1998; Brown, Wilson, Norcia & Boothe, 1998). However, VEP recordings while young infants view oscillating gratings and gratings moving only temporally-to-nasally or only nasally-to-temporally indicate that the VEP response is *greater* for N-T motion than for T-N motion (Mason, Braddick, Wattam-Bell & Atkinson, 1998). Thus cortical asymmetries as measured by VEPs are in the opposite direction to eye-movement asymmetries and cannot account for them (Mason et al., 1998). Moreover, infant monkeys show asymmetrical OKN until 3 weeks of age (Atkinson, 1979), but cells in the striate cortex of monkeys as young as 6 days old respond equally well to T-N and N-T motion (Hatta, Kumagami, Qian, Thorton, Smith & Chino, 1998). One possibility is that asymmetries favouring T-N motion originate further downstream in the cortical motion processing pathway, possibly in area MST (reviewed in Braddick, 1996). Thus, the reductions in OKN asymmetry that we observed might reflect changes in motion processing within structures beyond the striate cortex and/or their projections to the subcortical centres driving OKN.

A second hypothesis, proposed by Hoffmann (1986, 1989), states that asymmetrical OKN is caused by a lack of functional input from visual cortex to the nucleus of the optic tract (NOT) in the pretectum and the related dorsal terminal nucleus (DTN) of the accessory optic system. The NOT-DTN cells are the main link between sensory input from the retina and the motor output of OKN through the brainstem. These cells are binocular in normal adult cats and monkeys because they receive crossed input directly from the retina and both crossed and uncrossed input indirectly via the visual cortex (Hoffmann, 1982; Hoffmann, Distler, Erickson & Mader, 1988; Simpson, Giolli & Blanks, 1988; Hoffmann, Distler & Erickson, 1991). Although there is a direct retinal projection to the ipsilateral NOT-DTN, it is much smaller than the contralateral projection and its contribution to OKN is minimal. In cats, monkeys, and perhaps humans, the direct pathway from the retina through the contralateral NOT-DTN is sufficient to mediate OKN when patterns move temporally-to-nasally, especially when the movement is slow. The indirect pathway from the retina through the ipsilateral LGN and striate cortex to the ipsilateral NOT-DTN is necessary for consistent OKN when patterns move nasally-to-temporally (Harris, Leporé, Guillemot & Cynader, 1980; Montarolo, Precht & Strata, 1981; Hoffmann, 1982; Williams & Chalupa, 1983; Strong, Malach, Lee & Van Sluyters, 1984; Kato, Harada, Hasegawa, Igarashi, Koike & Kawasaki, 1986; Zee, Tusa, Herdman, Butler & Gücer, 1986, 1987; Simpson et al., 1988).

Hoffmann (1989) hypothesized that in cats, monkeys, and humans, OKN early in life is mediated entirely by subcortical projections to NOT-DTN which develop in the absence of visual experience and can mediate OKN for T-N motion. The cortical projections to NOT-DTN develop later. After the cortical projections are established, the subcortical projections lose influence over NOT-DTN cells. The reduction in subcortical influence occurs to a small extent in cats, to a greater extent in monkeys, and almost completely in humans. Psychophysical studies by Harris and colleagues that compared monocular and binocular responses to plaids support this evolutionary trend (Smith & Harris, 1991; Harris, Lewis & Maurer, 1993). Nonetheless, according to Hoffmann (1989), in all three species, OKN during infancy is asymmetrical because it is mediated by subcortical pathways. The notion of subcortical mediation in humans during early infancy is strengthened by independent evidence that the visual cortex is very immature at birth (Chugani, 1994; Huttenlocher, 1994; Braddick, Atkinson & Hood, 1996).

Thus, the decrease in OKN asymmetry that we observed likely reflects postnatal changes in the cortical input to NOT-DTN from striate cortex and/or from higher cortical areas in the motion processing stream. Our finding that OKN acuity is still asymmetrical at 2 years of age suggests that, even at that age, cortical input to NOT-DTN is still functionally immature. Our successful quantification of OKN asymmetry in individual normal infants suggests that this may be a useful tool for evaluating the degree of cortical insult caused by infantile ocular disorders such as strabismus or cataract. It might also be a useful tool for evaluating sensitive periods for the functional integrity of cortical input to the midbrain.

Future studies could test Hoffmann's hypothesis of subcortical mediation during early infancy more directly by measuring developmental changes in gain during the slow phase of OKN. Specifically, several investigators have argued convincingly that the slow phase of OKN is made up of two components: a rapid rise in the velocity of OKN that is mediated by cortical pathways and a slow rise in the velocity of OKN that is mediated subcortically, at least for slowly moving stimuli (Cohen, Matsuo & Raphan, 1977; Waespe, Cohen & Raphan, 1983; Zee et al., 1986; Zee et al., 1987; Schiff, Cohen & Raphan, 1988; Cohen, Schiff & Buettner, 1990; Cohen, Reisine, Yokota & Raphan, 1992). Onset of the rapid-rise component of OKN would mark the onset of cortical involvement in the mediation of OKN.

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