

Motion detection in normal infants and young patients with infantile esotropia [☆]

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Abstract

The purpose of this study was to investigate asymmetries in detection of horizontal motion in normal infants and children and in patients with infantile esotropia. Motion detection thresholds (% motion signal) were measured in 75 normal infants and in 36 eyes of 27 infants with infantile esotropia (ET), using a forced-choice preferential looking paradigm with random-dot patterns. Absolute motion detection sensitivity and asymmetries in sensitivity for nasalward (*N*) vs. temporalward (*T*) directions of motion were compared in normal and patient populations, ranging in age from 1 month to 5 years. In normal infants, *N* and *T* thresholds were equivalent under 2.5 months of age, whereas a superiority for monocular detection of *N* motion was observed between 3.5 and 6.5 months of age. The nasalward advantage gradually diminished to symmetrical *T*:*N* performance by 8 months of age, matching that of adults. No asymmetry was observed in 15 normal infants who performed the task binocularly, hence, the asymmetry was not a leftward/rightward bias. In the youngest infantile ET patients tested, at 5 months of age, a nasalward superiority in motion detection was observed and was equivalent to that of same-age normal infants. However, unlike normals, this asymmetry persists in older patients. This greater asymmetry in infantile ET represents worse detection of *T* than *N* motion. This is the first report of an asymmetry in motion detection in normal infants across a wide age range. Initially, motion detection is normal in infants with infantile esotropia. Cumulative abnormal binocular experience in these patients may disrupt motion mechanisms.

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1. Introduction

In the last few years, much has been uncovered about the maturation of sensitivity to motion during the first few months of life, using behavioral responses based on fixation (i.e., forced-choice preferential looking (FPL) and habituation), optokinetic nystagmus (OKN), and visual evoked potentials (VEP). These methods yield slight differences in the onset age for mo-

tion sensitivity, which depend upon the spatial and temporal properties of the stimuli used, but in general, it appears that the ability to discriminate different directions of motion in the absence of positional or orientational cues is apparent between 2 and 3 months of age using behavioral measures (Banton, Dobkins, & Bertenthal, 2001; Bertenthal & Bradbury, 1992; Braddick, Curran, Atkinson, Wattam-Bell, & Gunn, 2002; Dobkins & Teller, 1996; Wattam-Bell, 1996a; Wattam-Bell, 1996b) and slightly earlier for VEP (Hamer & Norcia, 1994; Wattam-Bell, 1991) and OKN (Manny & Fern, 1990).

In neonates, the OKN response is stronger for motion in the nasalward (*N*) direction than the temporalward (*T*) direction (Atkinson, 1979; Naegel & Held,

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1982), which is believed to arise from the directionally selective cells in the pretectal nucleus of the optic tract (NOT) and the dorsal terminal nucleus (DTN) of the accessory optic system (Hoffmann, 1981; Hoffmann, Bremmer, Thiele, & Distler, 2002). The asymmetric OKN response is mediated by a direct pathway from the retina to the contralateral NOT–DTN, in which cells are strongly selective for ipsiversive stimulus movement (i.e., the right NOT–DTN prefers rightward movement and the left NOT–DTN prefers leftward movement). OKN becomes symmetric for both directions of stimulation between 3 and 6 months, with symmetry typically reached later for faster velocities (Lewis, Maurer, Smith, & Haslip, 1992; Mohn, 1989; and see Distler, Vital-Durand, Korte, Korbmacher, & Hoffmann, 1999 for similar findings with macaque monkeys). The emergence of symmetry has been attributed to the contribution of the subcortical structures becoming dominated by progressively maturing binocular connections from the cortex, particularly area MT, to the NOT–DTN (Harris, Lewis, & Maurer, 1993; Hoffmann, 1998; Hoffmann et al., 2002; Roy, Lachapelle, & Lepore, 1989).

In normal infants, a nasal–temporal asymmetry is also observed in the steady-state motion VEP response to an oscillating vertical grating (Birch, Fawcett, & Stager, 2000; Hamer & Norcia, 1994; Jampolsky, Norcia, & Hamer, 1994; Mason, Braddick, Wattam-Bell, & Atkinson, 2001; Norcia et al., 1991). The motion VEP asymmetry is robust from 2 to 5 months of age and diminishes with age, although the exact age depends on spatial and temporal stimulus parameters, i.e., earlier for lower spatial and temporal frequencies (Norcia, 2004). However, prior to 1.5 months of age, no asymmetry is observed in the motion VEP (Birch et al., 2000) nor is an asymmetry found in infants' looking preference for *N* vs. *T* motion (Wattam-Bell, 2003), despite the fact that the OKN is reported to be asymmetric at this age (Atkinson, 1979). This may result because the OKN is mediated by the asymmetric NOT–DTN, while cortical structures (V1, V5, and MT) are not yet mature enough to manifest an asymmetry or because connections between the asymmetric NOT–DTN and motion sensitive cortical structures are not mature. Currently, no psychophysical data is available to address whether the asymmetry is observed in motion detection thresholds in early visual development. Therefore, one aim of the present study was to investigate perceptual motion asymmetries in normal infants, across a wide range of ages, by obtaining detection thresholds separately for *N* and *T* motion.

Mounting evidence suggests that motion processing is affected in binocular disorders such as strabismus. Abnormal motion processing, particularly a nasal–temporal asymmetry in processing horizontal motion, has been reported in adult patients with a history of strabismus. Specifically, asymmetries in this population have

been reported in OKN (Reed et al., 1991; Roberts & Westall, 1990; Schor, Fusaro, Wilson, & McKee, 1997; Schor & Levi, 1980; Valmaggia, Proudlock, & Gottlob, 2003; Westall et al., 1998; Westall & Shute, 1992), velocity judgments (Brosnahan, Norcia, Schor, & Taylor, 1998; Tychsen & Lisberger, 1986), motion detection (Fawcett, Raymond, Astle, & Skov, 1998; Shallo-Hoffmann et al., 1997), and smooth pursuit (Tychsen & Lisberger, 1986). In these studies, the asymmetrical performance in adult patients with infantile esotropia (ET) generally reveals a weak response for temporalward motion. Moreover, adults and infants with early abnormal binocular experience show asymmetries in motion VEP responses (Birch et al., 2000; Fawcett & Birch, 2000; Jampolsky et al., 1994; Norcia et al., 1991; Norcia, Hamer, Jampolsky, & Orel-Bixler, 1995; Shea, Chandna, & Norcia, 1999). One limitation of studies in adults is that many of the patients have an unknown age of onset and undocumented treatment histories, so it is difficult to determine whether the deficits are primary, secondary to abnormal visual experience, or secondary to treatment. Currently, no perceptual data are available to determine whether perceptual asymmetries are associated with infantile ET prior to or following treatment. Therefore, the second aim of the current study was to evaluate motion detection in infants and children diagnosed with infantile ET, early in the course of the disease.

2. Methods

2.1. Subjects

A total of 88 normal infants and children were enrolled, with testing aborted for 13 fussy or sleepy infants, leaving 75 normal subjects who provided data; 60 were tested monocularly and 15 were tested binocularly as a control. Average age was 8.8 months, ranging from 1.0 to 56.1 months of age. Eleven of the 60 subjects tested monocularly provided data on more than one visit. Twenty-seven patients with infantile ET participated, providing a total of 36 visits, with a mean age of 23.3 months, ranging from 4.4 to 60.0 months of age. Subjects were grouped by age, to create six age groups, in postnatal months: 0.5–2.0; 2.0–3.5; 3.5–6.5; 6.5–9.5; 9.5–26.5; 26.5–60.0 (see Table 1). The mean ages in each group falls on a roughly logarithmic spacing (with a log base of 1.5), to account for rapid (and more interesting) changes early and slower changes later. (Since the diagnosis of infantile ET is rarely made prior to 4 months of age, no patients were available in the two youngest age groups.) Five adults with normal or corrected-to-normal acuity and stereoacuity also provided control data.

All participants were born within 14 days of their due dates, with no ocular or neurological abnormalities, and

Table 1

Age groups for normal infants and infants with infantile ET who provided monocular motion detection thresholds for this study

Age group (months)	Normal infants, $N = 75$			Infantile esotropia, $N = 36$		
	Mean age	Real age range	N	Mean age	Real age range	N
Under 2.0	1.6	0.99–2.0	5	–	–	0
2.0–3.5	2.6	2.1–3.5	16	–	–	0
3.5–6.5	4.9	3.7–6.3	26	5.1	4.4–6.4	5
6.5–9.5	8.3	6.7–9.4	11	8.1	7.3–9.2	7
9.5–26.5	13.8	10.7–24.0	12	16.3	9.7–26.0	14
Over 26.5	44.3	28.0–56.1	5	44.5	29.2–60.0	10

An additional 15 normal infants were tested binocularly, providing thresholds for each direction. No infants with infantile ET were available for testing before 4.4 months of age. Repeat visits are included in the table.

no manifest nystagmus. All had normal acuity in both eyes, assessed with Teller acuity cards or crowded optotypes on the same visit.

All patients had onset of infantile ET with an initial deviation 30–65 p.d. by 6 months of age with confirmation by a pediatric ophthalmologist by 8 months of age. Median age of onset was 3 months of age. Sixteen of the patients had infantile ET, with constant esodeviation of 30 p.d. or greater and low hyperopia ($\leq +2.00$ D), and six had infantile partially accommodative ET (a decrease in angle of deviation of ≥ 10 p.d. and a residual angle of ≥ 20 p.d. with full hyperopic correction). From these patients, 11 eyes (from 11 patients) were tested prior to surgery and 20 eyes (from 11 patients) were tested after surgery. Surgically treated patients had alignment within 8 p.d. An additional five patients had infantile accommodative ET that was fully corrected to orthophoria with glasses, prior to testing.

Informed consent was obtained from one or both parents prior to the infant's participation. This research protocol observed the tenets of the Declaration of Helsinki and was approved by the Institutional Review Board of the University of Texas Southwestern Medical Center.

2.2. Stimuli

The stimuli were random-dot patterns (RDPs) similar to those used by Wattam-Bell (1996a), programmed with MATLAB 5.2.1. Two RDPs were presented side-by-side on a 20 in. Trinitron Multiscan 520GS monitor, with a refresh rate of 75 Hz. Each RDP was 20° by 11.5° , with their inner edges separated by 18.4° . Within each RDP, white (102 cd/m^2) dots were presented against a black (3 cd/m^2) background. Dots were 0.32° by 0.32° in size, and dot density (area of pattern illuminated by white) was 5.0%. These two patterns were surrounded by a gray background, at a luminance equal to that of the mean luminance of the pattern.

The two RDPs were divided into three equally-sized top, middle, and bottom segments (6.7° by 11.5°) as illustrated in Fig. 1. In one of the two RDPs, the top and bottom segments contained stationary dots while

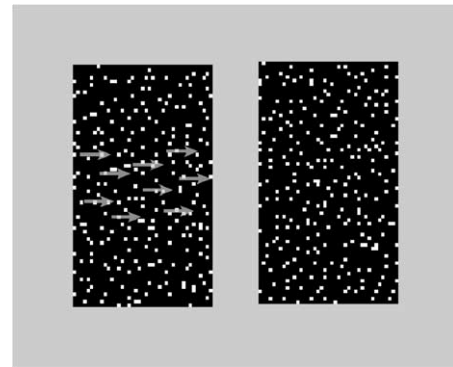


Fig. 1. Illustration of the stimulus showing a rightward moving random-dot pattern on the left side. If viewing monocularly with the right eye, this would be temporalward motion. The target was a middle one-third segment, with the upper and bottom two segments containing stationary dots. On each trial, the target was presented on the left or right side and contained dots moving either rightward or leftward.

the middle segment contained a variable proportion of moving and stationary dots. All moving dots in the middle segment moved “coherently” (at the same temporal and spatial displacement) in one direction, either leftward or rightward, at a velocity of $10^\circ/\text{s}$ with an unlimited lifetime. Once a dot completed its motion trajectory, it wrapped around in a new random location. The density of the display was sparse enough that no collision or overlap between dots was noted by the authors. The other RDP had stationary dots across all three segments.

Our stimuli and task were chosen to permit measurement of motion detection thresholds with preferential looking in very young infants and in patients with strabismus who may have abnormal motion perception. Although the RDP stimulus pairs used in our study do not require reliance upon directionally selective motion mechanisms per se, this stimulus proved to be very testable with newborns. Moreover, we reasoned that any systematic difference between nasalward and temporalward motion sensitivity is likely to emerge from motion-specific pathways, since flicker detection mechanisms are not expected to show such asymmetries in sensitivity for direction of motion.

2.3. Procedure

All subjects were tested at a viewing distance of 40 cm. All normal participants were tested monocularly, with the non-viewing eye occluded with an orthoptic patch. For the normal young and adult participants, the eye tested was picked randomly; for patients, the preferred eye was tested. In cases when normal infants/children were uncooperative with monocular occlusion ($n = 15$), motion detection thresholds were obtained with both eyes open; these data are noted separately from monocular thresholds.

2.3.1. Infant testing

Infants were seated on the parent's lap in front of the monitor. At the beginning of each trial, a moving white fixation square (size = 2.3°) oscillated up and down along with a synchronized auditory tone to attract the infant's attention to the center of the monitor. Once the infant's gaze was in the center, the experimenter initiated the trial, the fixation square disappeared, and the stimuli were immediately presented. The experimenter, standing behind the monitor, observed the infant's head and gaze position under the diffuse light from the monitor in an otherwise dark room. The direction of motion and the location of the moving target on any given trial were randomized and unknown to the experimenter. The experimenter made a judgment about whether the infant oriented to the right or left side of the monitor based upon the first fixation away from center. This precluded using the reflection of the moving stimuli in the infant's pupil or OKN as a cue to the target's actual location.

2.3.2. Adult testing

Adults were instructed to report which side the segmented target appeared, on the left or right side. They recorded their responses with a joystick (turned to the right or left to match location of the target). To make the testing condition more similar to that used for infants, adults were asked to generally fixate in the center during stimulus presentation (although the fixation spot had disappeared at this point). This is to ensure that adults do not make comparative saccades between the two locations. If adults were to break fixation, they were instructed to enter their first response. In addition, adult subjects were asked to make their response within 5 s. Despite these attempts to make testing more difficult, all adults were able to accurately identify the location of the segmented target even at the minimum stimulus level available (1% motion).

Thresholds for both infants and adults were obtained using a 2 spatial-alternative 2-down-1-up staircase procedure (Birch & Swanson, 1992), varying the percentage of coherently moving dots in the middle segment of one RDP on each trial. After an initial screening phase using

a step size of 2 log units, the staircase proceeded at 1 log unit steps. Staircases for N motion and for T motion were interleaved across trials, such that both staircases were obtained within one testing session. A total of six staircase reversals were obtained for each motion direction. On average, each session required 42 trials to complete both staircases (range: 28–64). When subjects thresholds were at the maximum stimulus level available, the MATLAB program reverted to a block method (Birch & Swanson, 1992). A maximum likelihood fitting procedure was used to fit a Weibull function (Weibull, 1951) to the plot of percentage of correct responses against percentage of moving dots, separately for each direction of motion. Threshold for each direction of motion was defined as the percentage of dots corresponding to 75% correct performance. Each subject contributed two motion detection thresholds, N and T , within each testing session. To assess relative N vs. T performance, a log $T:N$ threshold ratio was calculated for each subject.

2.3.3. Statistical analyses

Comparison of N and T motion detection thresholds in normal infants and children was conducted using a 4×2 mixed-factor ANOVA with age group as a between-subjects variable and direction-of-motion as a repeated factor. Log $T:N$ threshold ratios as a function of age in normal infants/children were evaluated using a one-way ANOVA and with post-hoc Duncan's multiple range tests to identify significant differences between pairs of age groups, while maintaining the overall alpha at a probability of 0.05. When comparing treatment groups vs. normals, ANOVA's and unpaired t tests were conducted between groups, only including matched age groups.

3. Results

3.1. Motion detection in normal infants

3.1.1. Motion detection thresholds

Fig. 2 shows the mean motion detection thresholds for normal infants, for each age group. Lower threshold values indicate a lower signal needed to attain 75% correct, hence, better performance. A significant main effect was found for age group ($F(5, 69) = 19.85$; $p < 0.00001$), indicating a dramatic improvement in overall motion detection with age. A significant interaction between age group and direction-of-motion indicates that the decline in thresholds with increasing age is different for N and T directions of motion ($F(5, 69) = 4.53$; $p < 0.001$). As is apparent in Fig. 2, this interaction is a result of the more rapid improvement in N than T thresholds. That is, sensitivity to nasalward motion matures sooner, reaching asymptote in the 3.5–6.5 month age group,

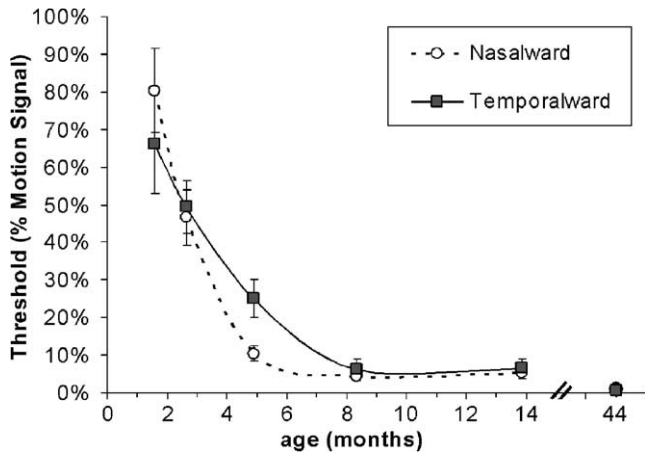


Fig. 2. Mean *N* and *T* motion detection thresholds for normal infants ($n = 75$), with percent motion signal plotted against age in months. Each line represents mean *N* (open circles) and *T* (filled squares) thresholds for each age group. Error bars represent the standard error of the mean.

while sensitivity to temporalward motion reaches maturity in the 6.5–9.5 month age group. A rapid emergence of motion detection was observed when comparing overall motion sensitivity with increasing age groups. At 4 and 10 weeks of age, four infants provided thresholds near ceiling (95–100% motion signal), while the other six subjects under 10 weeks of age (as well as all older subjects) were capable of providing lower thresholds. Collapsing across direction-of-motion, the overall average threshold for five infants aged 1.0–2.0 months of age was 73% motion signal. In infants 2.0–3.5 months

of age, mean threshold decreased by approximately half to 48%. In infants 3.5–6.5 months of age, average threshold again halved to 20%, and by 6.5 months of age, mean threshold was 5%.

3.1.2. Nasalward vs. temporalward asymmetry

Log *T:N* threshold ratios were averaged for each age group and are presented (as a bold line) in Fig. 3. Eleven infants who returned for repeat visits are also plotted in the figure. For ease of viewing of the younger ages, age plotted on the *x* axis is truncated at 24 months, omitting the oldest age group, as no change occurs beyond 9.5 months. Symmetrical *N* and *T* performance is equivalent to a log *T:N* threshold ratio of 0.0, in which thresholds for *N* and *T* directions-of-motion are identical. Positive log ratios indicate better performance (i.e., lower thresholds) for *N* than *T* direction of motion. The mean log ratio for five adults was 0.0, i.e., symmetrical performance.

Most notably, the mean data from normal infants showed a nasalward superiority at 3.5–6.5 months of age, and symmetrical *T:N* performance for the younger and older ages. A significant main effect of age group on log threshold ratios was observed ($F(5, 69) = 4.69$; $p < 0.001$). The mean log ratio for the 3.5–6.5 month old age group was significantly larger than each of the other five age groups (Duncan’s multiple range test, $p < 0.03$). All other age group pairs were not significantly different from one another.

In the 10 youngest infants tested between 0.99 and 2.2 months of age, mean log ratio was -0.04 ($SD = 0.13$) and in 11 infants tested between 2.50 and 3.45 months

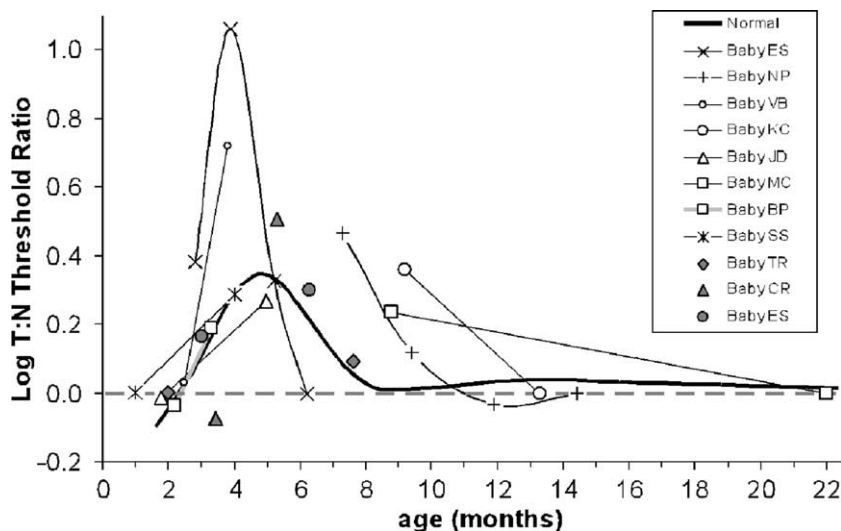


Fig. 3. Mean log *T:N* threshold ratios for normal infants (thick solid line with no symbols), as well as 11 infants who returned for repeat visits. For ease of viewing of the younger ages, the error bars are omitted (but are present in Fig. 6), and age plotted on the *x* axis is truncated. The dotted line indicates a log *T:N* ratio = 0.0. Ratios >0.0 indicate worse detection of *T* than *N* motion direction. For 8 of the longitudinal infants, a line connects their visits, while in three infants with only two visits (filled symbols), no line is present in order to arbitrarily illustrate a possible fit to the developmental course suggested by the data, rather than a direct developmental trajectory between these two points.

of age, mean log ratio was 0.06 (SD = 0.24). In both of these groups combined, seven had positive log ratios, four were symmetrical, and 10 had negative log ratios. Thus, overall, performance for N and T directions-of-motion was equivalent under 3.45 months of age. From 3.5 to 6.5 months of age ($n = 26$), T threshold was on average 3.9 times worse than N threshold. In this age group, 81% (21/26) of the infants had positive log $T:N$ ratios, indicating a nasalward superiority, while 15% (4/26) had negative log ratios. For infants over 6.75 months of age ($n = 28$), the mean log ratio corresponds to 0.01 (SD = 0.25), which is near adults' symmetrical performance.

It could be argued that the lack of asymmetry in the youngest infants is due to very poor performance. However, even after eliminating the data from eight infants in the youngest age group whose thresholds were worse than 50% motion signal, the mean log ratio for the remaining 13 infants under 3.5 months of age (mean age = 2.68) was 0.03 (SD = 0.23), which is not significantly different from zero ($t(12) = 0.54$, $p = 0.59$). Of these, 46% (6/13) had positive ratios, and 38% (5/13) had negative ratios. Infants have poor resolution acuity, and in this study, infants under 3.5 months had an average acuity of 0.83 logMAR based on the Teller acuity cards, with the worst acuity being 20/400, however, this is not expected to alter the results. We simulated 20/400 vision in two adults with defocusing lenses, and this had no effect upon performance.

3.1.3. Longitudinal data

The development of a nasalward asymmetry is also observed in longitudinal data from 11 infants. Nine infants had a second follow-up visit, while two infants had four visits each. For eight infants, a line is plotted in Fig. 3 to show the change in log $T:N$ ratio over time, while in three infants with just two visits, no line was plotted, in order to illustrate the possible fit to the developmental course suggested by the data, rather than a direct line between these two points. These data agree with the overall developmental course of a nasalward advantage that first emerges at approximately 2.5 months of age, peaks around 3.5–4 months of age, declines at 6 months of age, and is nearly absent at 8 months of age.

3.1.4. Binocular vs. monocular thresholds

As can be seen in Fig. 4 there was no difference in thresholds obtained binocularly ($n = 15$) for rightward vs. leftward direction of motion ($t(14) = 1.31$; $p = 0.21$). Infants tested binocularly had a mean age of 6.8 months and range in age from 0.49 to 12.3 months, including the age range in which the asymmetry is observed monocularly. The monocular N and T thresholds for all normal infants (OD $n = 42$; OS $n = 33$) also are replotted as rightward and leftward directions of motion in Fig. 4, and there is no difference in these thresholds,

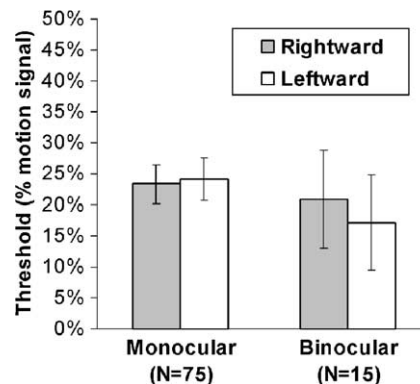


Fig. 4. Mean thresholds presented for each direction of motion as rightward vs. leftward, for two samples of normal infants, those tested monocularly ($n = 75$, from main experiment) and binocularly ($n = 15$).

for either eye (t tests: OD, $p = 0.40$; OS, $p = 0.25$). Even when the analysis is limited to infants in the age range of 3.5–9.5 months (in order to include only the age range in which the nasalward advantage was observed), there was still no difference between rightward and leftward directions ($p = 0.46$), yet detection of N motion is significantly better than T motion for each eye in this age group (OD, $p = 0.03$; OS, $p = 0.05$).

3.2. Infantile esotropia

3.2.1. Motion detection thresholds

To compare overall motion sensitivity in normal infants and patients with infantile ET, mean thresholds are plotted in Fig. 5. In order to match all four subject

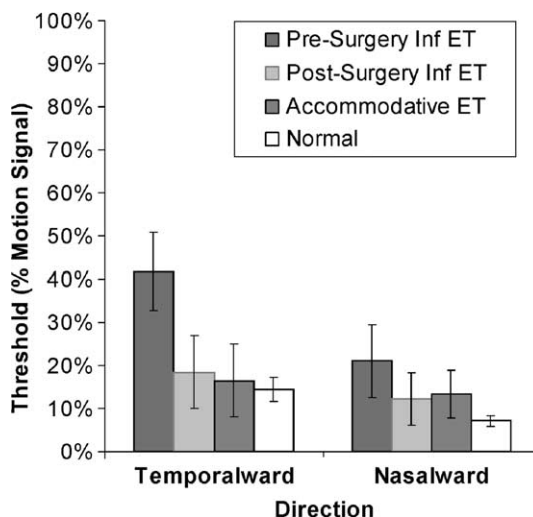


Fig. 5. Mean motion detection thresholds for each subject group (error bars denote SEM). Infantile ET patients are separated based on treatment. In order to match each group for the same-age range, subjects included in each group is confined to 4–24 months of age. Mean ages (in postnatal months) for each group: pre-surgery ($n = 11$) = 9.3; post-surgery ($n = 20$) = 12.2; accommodative ($n = 5$) = 17.0; normals ($n = 46$) = 8.1. No significant difference in age was observed ($F < 1$, $p = 0.69$).

groups for age, only participants within 4–24 months were included in this analysis. Overall, pre-surgery patients with infantile ET had significantly higher detection thresholds (i.e., worse performance) than normals ($F(1, 55) = 8.42; p = 0.005$). Pre-surgery patients' mean thresholds were 21% and 42% while similarly aged normals' thresholds were 7% and 14% motion signal for *N* and *T* motion, respectively. When examining performance at more specific ages, this difference between pre-surgery patients and normals was significant for *T* direction at 5 months ($p = 0.05$) and 8 months ($p = 0.03$) but not at 14 months of age ($p = 0.10$). For the *N* direction, normals and patients were not significantly different at any age group.

As seen in Fig. 5, motion detection thresholds of post-surgery infantile ET patients and patients with infantile accommodative ET (corrected with glasses) were intermediate to the pre-surgery and normal subjects and did not differ significantly from either group ($F < 1.2; p > 0.05$). Post-surgery patients were substantially better than the pre-surgery patients for *T* motion thresholds (42% vs. 18%), and this was significant ($p = 0.04$). Post-surgery patients were also better than pre-surgery patients for *N* motion thresholds (21% vs. 12%), however, this difference was not significant ($p = 0.20$).

3.2.2. Nasalward–temporalward asymmetry

Log *T:N* threshold ratios for patients with infantile ET are presented in Fig. 6, with data for normals replotted. Initially, when tested at 4–5 months of age, pre-surgery infantile ET patients were similar to normal controls ($F < 1$). That is, both subject groups had a four-fold superiority in detection of *N* motion over *T* motion

at this age. At 8 and 14 months of age, pre-surgery infantile ET patients had abnormally large ratios, which were significantly greater than similarly aged normals' ($F(1, 26) = 13.0; p = 0.001$). Neither post-surgery ET patients ($F(1, 46) = 3.33; p = 0.07$) nor patients with corrected accommodative ET ($F < 1$) differed significantly from similarly aged normals. Pre- and post-surgery patient groups (at 8 and 14 months) were not significantly different from one another ($F(1, 15) = 3.78; p = 0.07$).

In order to quantify the prevalence of asymmetry in both the normal and patient groups, the 95% tolerance limits for symmetry was constructed based on the data from 17 normal infants with ages 9.5–52 months, in which their performance was very similar to adults' and past the asymptote in developmental change. (Note adult performance could not be used to calculate tolerance limits, as performance was at minimum.) The 95% tolerance limits were defined as two standard deviations above/below the mean log ratio from these mature infants. Fig. 7 shows the percent of normal controls and patients with infantile ET in each age group who had log threshold ratios that exceeded the upper tolerance limit; i.e., showed significantly asymmetric motion detection thresholds. At 5 months of age, 60% of normals had abnormally large ratios, and at all other ages this percentage was between 0% and 20%. Most notably, patients with infantile ET who had not had surgery had a similar prevalence to normals at 5 months of age, however, the prevalence remains higher than that of normals in all age groups thereafter. The infantile ET patients who had been successfully treated with glasses or who had surgical reduction of misalignment look remarkably like normals.

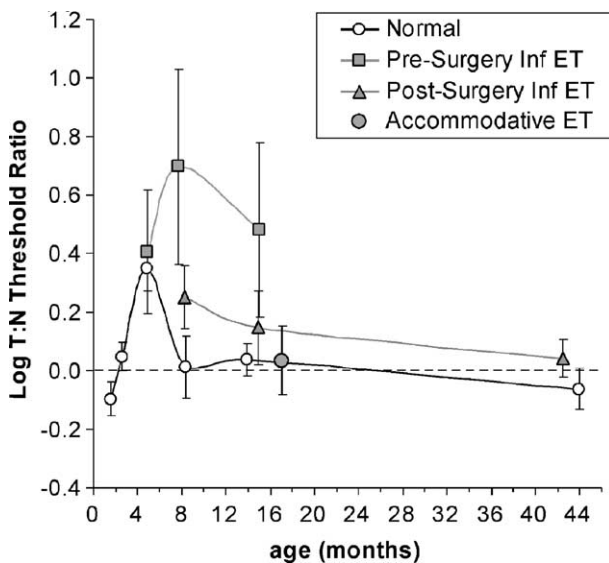


Fig. 6. Mean log *T:N* threshold ratios for all normal infants (open circles; replotted from Fig. 3, with all age groups, $n = 75$) and infantile ET patients (filled symbols; $n = 36$), separated by treatment, see text. Each data point represents mean ratios from infants at each age group.

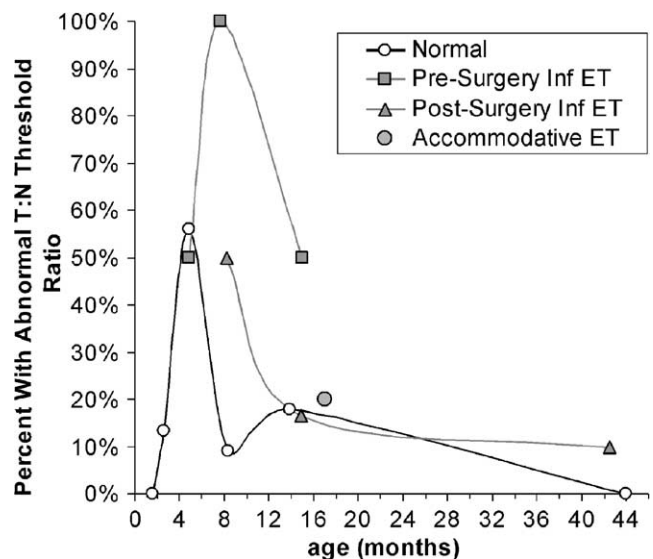


Fig. 7. Percent of normal infants (solid line open circles) and infants with infantile ET (gray line, filled circles) within each age group with significantly “abnormal” threshold ratios (see text).

4. Discussion

4.1. Normal maturation of motion sensitivity

In this study, normal infants show rapid development of motion detection during the first 6 months of life. The youngest infants, at 5 weeks of age, performed at maximum (around 100% motion signal). Thresholds dropped to 50% by 2 months of age, continued to decline dramatically at 5 months of age, and reached near-asymptote at 8 months of age. The present results agree with other reports that the earliest sensitivity to opposite directions is evident in infants' looking behavior between 6 and 8 weeks of age (Aslin & Shea, 1990; Banton et al., 2001; Bertenthal & Bradbury, 1992; Roessler & Dannemiller, 1997; Wattam-Bell, 1991; Wattam-Bell, 1996a; Wattam-Bell, 1996b). Early immaturity of motion processing has also been noted in macaque, in which directionally selective cells in V1 narrowed in tuning between day 6 and week 4 of age (Hatta et al., 1998). Using the common 4:1 ratio of age for human:macaque, this period corresponds to 0.8–3.5 months of age in humans.

In the youngest infants under 2.5 months of age tested in this study, *N* and *T* thresholds were symmetrical, and roughly equal proportions of infants fell on either side of symmetry (i.e., log ratio = 0.0). Poor acuity or poor motion thresholds could not explain this symmetrical performance, since symmetrical performance was observed in infants who performed very well, and reduced acuity to 20/400 with optical blur had no effect upon adult performance. Similarly, Wattam-Bell (2003) found that 5–6 week old infants were symmetric in their preference for viewing *N* vs. *T* direction of motion, using a slightly faster velocity (18.8 %/s to our 10 %/s). Birch et al. (2000) also failed to find monocular horizontal VEP asymmetry under 1.5 months of age. On the other hand, OKN is asymmetric at this age (Atkinson, 1979; Naegele & Held, 1982). The absence of asymmetry in motion detection during the first weeks of life suggests that the asymmetry observed in OKN is independent of the asymmetry observed in motion detection. This is congruent with previous reports of independence among asymmetries in OKN, motion VEP, and preferential looking (Mason, Braddick, & Wattam-Bell, 2003; Mason et al., 2001). Since it is generally accepted that neonatal OKN is mediated subcortically, this suggests that the motion detection asymmetry is cortical in origin.

In contrast to the neonatal stage, between 3.5 and 6.5 months of age, 56% of normal infants had a significant nasalward bias while only 8–17% of normal infants in all other age groups had a significant nasalward bias. Longitudinal data from a subset of infants shows that the maturational pattern is present within individuals as well as in the cross-sectional survey. Results from infants and children tested binocularly confirmed that no asymmetry was observed for leftward or rightward mo-

tion. The asymmetry observed in this study diminished with age after 6.5 months of age. Asymmetrical responses in OKN, smooth pursuit, and motion VEPs similarly become symmetrical at about 6 months of age.

The age at which a symmetrical or mature response is reached for motion VEP, monocular OKN, motion discrimination is dependent upon spatio-temporal properties of the stimuli. One may ask whether our lack of asymmetry at the youngest ages tested was due to our choice of motion dot speed; specifically, with a faster velocity, perhaps an asymmetry could be observed in infants under 3.5 months (and likewise, after 6 months of age). Although this idea would fit with the finding that symmetrical or mature responses in monocular OKN (Mohn, 1989; Roy et al., 1989; and Distler et al., 1999 with monkeys) and motion VEP (Wattam-Bell, 1991) are obtained at later ages for faster speeds, it does not account for why the asymmetry is first absent and later appears later at 3.5 months for the same speed in this study.

Regarding our observed shift from neonatal lack of asymmetry to asymmetrical motion detection in 3.5–6 months old, it may be that initially these infants lack cortical directional mechanisms, and when directional selectivity emerges, an asymmetry is initially present. It is equally plausible that while neonates do have directionally selective mechanisms, the most sensitive mechanisms for the stimuli employed in our task are non-directional flicker detectors, which are later superseded by asymmetric directional mechanisms. However, in the light of other results, the first alternative is the most likely. Dobkins and Teller (1996), using a summation-at-threshold paradigm, found that in 3 month old infants, the most sensitive mechanisms for detection of motion are also directionally selective, which is what the present results suggest as well for the 3.5–6 month period. Following 6 months of age, symmetrical performance is observed which is likely to be due to maturation of binocular connections.

Differences between the maturational courses for OKN and other aspects of motion processing may reflect the maturational rates of distinct motion pathways. At birth, only the subcortical mechanism is functional and asymmetric; this mechanism mediates early OKN responses. Thus, neonatal monocular OKN asymmetry has been attributed to the earlier maturation of retinal projections to the directionally selective cells in the NOT–DTN; the direct retinal projections to the contralateral NOT–DTN mature faster than the indirect cortical projections carrying ipsilateral retinal input (Distler & Hoffmann, 2003; Hoffmann, 1981). Symmetry of OKN responses is attributed to the binocular cortical input to cells in NOT–DTN. Motion detection and motion VEP responses, on the other hand, are dominated by activity in early visual cortical areas, possibly with an additional contribution of extrastriate areas (V5/

MT) to motion preferences and motion discrimination. Braddick (1996) argues the source of the nasal–temporal asymmetry may be located in MST, and early in the course of development, the directional tuning is limited to a few directions. This limited range causes an asymmetry, and as this range expands later, the asymmetry diminishes. Although no support has yet been found for this asymmetrical development of directional tuning, a possible source for the cortical asymmetry is suggested by the electrical stimulation and single-cell recording results of Hoffmann et al. (2002). They found that cells in MT, MST, and V1 project to NOT–DTN and these cells have ipsiversive directional preference (i.e., towards the recording site), which could account for the immature nasal–temporal motion VEP asymmetry as well as the motion detection asymmetry observed here. Only those cells that project to NOT–DTN were found to have this ipsiversive directional preference, and this selectivity was not reflected in the area as a whole. This could explain why no asymmetries in overall directional preference were found in single-cell recordings in V1 neurons of infant rhesus monkeys (Hatta et al., 1998) and in MT neurons (Kiorpes, Walton, Movshon, & Lisberger, 1996) of adult strabismic monkeys. Alternative hypotheses for a cortical asymmetry are that there may be an asymmetry in the population of directional mechanisms, such as smaller numbers and/or weaker responses of neurons tuned to temporalward motion or that the subcortical asymmetry may indirectly affect cortical responses.

4.2. Infantile esotropia

Overall, the participants with untreated infantile ET in this study were significantly worse than normals at detecting temporalward direction of motion, which was observed at all ages tested. At 8 and 14 months of age, corresponding ages when normals are symmetrical in detection of *N* and *T* motion, pre-surgery infantile ET patients had abnormally larger asymmetries, with worse detection of *T* than *N* motion. This was also evident in a larger proportion of pre-surgery patients with abnormal asymmetries at 8 and 14 months of age.

Young patients with infantile ET who had been treated early with surgery or glasses appear to have symmetrical performance similar to normals. These findings of reduced asymmetry with early treatment are in agreement with several mVEP studies (Fawcett & Birch, 2000; Jampolsky et al., 1994; Norcia et al., 1995). In infant monkeys with optically-induced strabismus, benefits of early alignment (corresponding to 6 months of age in humans) are observed for mVEP as well as for OKN and pursuit (Tychsen, Wong, Foeller, & Bradley, 2004; Wong, Foeller, Bradley, Burkhalter, & Tychsen, 2003). Motion VEP asymmetries persist in adult patients with early-onset strabismus who were treated after 2 years of age (Norcia et al., 1991), and these asymmetries

are reduced in infants treated in the first 10 months of life (Birch et al., 2000).

We also tested two late-onset esotropic patients (onset age: 12 and 36 months; not included in the main study), and neither showed a motion detection asymmetry (log threshold ratios were 0.0 and -0.4). This absence of an asymmetry in late-onset strabismus agrees with previous reports with other measures of motion sensitivity, including motion VEP (Brosnahan et al., 1998; Fawcett & Birch, 2000; Hamer, Norcia, Orel-Bixler, & Hoyt, 1993), monocular OKN (Demer & von Noorden, 1988; Steeves, Reed, Steinbach, & Kraft, 1999; Westall & Shute, 1992), pursuit eye movements (Sokol, Peli, Moskowitz, & Reese, 1991; Tychsen, Hurtig, & Scott, 1985) and velocity perception (Tychsen, Rastelli, Steinman, & Steinman, 1996).

At 4.5–6 months of age, pre-surgery infantile ET patients were not different from normal controls in exhibiting a strong nasalward advantage. This important fact indicates that the presence of the nasalward motion detection asymmetry is not a primary deficit associated with infantile ET. Like our findings, young strabismic patients, at 4–6 months of age shortly after onset of the disease, appear to have the capacity for normal stereopsis (Birch & Stager, 1985) and normal (albeit asymmetric) motion VEP responses (Birch et al., 2000). After 6 months of age, the motion detection asymmetry declines sharply in normals to reach symmetry by 8 months, while the asymmetry *increases* sharply in patients with untreated strabismus, and remains high thereafter (see Figs. 6 and 7). A persistent asymmetry after 6 months of age in infants with esotropia is also observed in cortical VEP responses to horizontally moving patterns (Fawcett & Birch, 2000; Norcia et al., 1991). Thus, for various sensory measures, it appears that the youngest infantile ET patients, diagnosed shortly after onset, and early in the course of treatment, are similar to normal cohorts. This suggests that initially in the course of the disease, sensory development is normal. Either the absence of normal binocular experience or prolonged abnormal binocular experience appears to preclude resolution of the asymmetry or to increase the asymmetry.

Fu and Boothe (2001) found abnormal/deficient temporalward and normal nasalward motion detection in monkeys reared with alternating monocular occlusion. They used a directional task in which monkeys were trained to discriminate coherent from random motion in a random-dot display. Although our task does not unequivocally isolate directional mechanisms, the similarity in the two studies bolsters the conclusion that the abnormal asymmetry is a result of impaired temporalward motion detection, relative to normals.

Other evidence showing that motion perception may be disrupted by abnormal binocular experience comes from early enucleated subjects who have abnormal

motion perception in the remaining eye—both poorer thresholds for detection motion-defined form and a nasalward asymmetry in detection of coherent motion (Steeves, Gonzalez, Gallie, & Steinbach, 2002). Many findings point to a developmental link between cortical motion processing and binocular sensory experience. However, the relationship between motion VEP asymmetry, which is taken to be a measure of cortical motion processing, and motion perception within individuals and how these measures are affected by infantile ET have yet to be clarified.

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