

MINIREVIEW

DEVELOPMENT OF CONJUGATE HUMAN EYE MOVEMENTS

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(Received 20 July 1987)

Abstract—Early studies of the development of oculomotor control in human infants relied on descriptions of eye movements. Recently, studies have been carried out using eye movement recording techniques typically used with adults. This review first considers the limitations of such techniques, especially as they are used with human infants, and then discusses the results of recent studies of human oculomotor development.

Infants Humans Eye movement Saccades VOR Smooth pursuit Development OKN

INTRODUCTION

The visual capacities of human infants less than a year old once were thought to be quite rudimentary but now appear to be more adultlike than had been expected (see Boothe *et al.*, 1985, for a review). However, the ability of an infant to extract visual information from the world around her depends in part on her ability to move her eyes. Unfortunately, relatively little is known about the development of oculomotor control. Early studies relied primarily on qualitative descriptions of infant oculomotor behavior. Only recently have attempts been made to record infant eye movements under controlled conditions similar to those used for testing adults. This review first considers the limitations of the techniques used to measure conjugate eye movements in human infants and then discusses the rather primitive state of our knowledge about oculomotor development.

EYE MOVEMENT MEASUREMENT

Infant eye movements are recorded almost exclusively either with the electrooculogram (EOG) or some variation of a corneal reflection method. Other more sensitive and accurate methods are used on adults (see Young and Sheena, 1975, for a review) but they are either too intrusive (e.g. electromagnetic search coils) or require too much subject cooperation (e.g.

double Purkinje image tracker). Each technique used with infants has certain advantages and disadvantages, which we will discuss first. However, both techniques share the disadvantage that the recordings must be calibrated in order to obtain quantitative information about eye movements; calibration techniques unique to infants will be discussed second. Finally, even when calibrated eye movements can be obtained, the interpretation of oculomotor behavior in infants presents a variety of special problems that must be surmounted; these are considered last.

Techniques and their limitations

EOG. The EOG measures the position of the eye with respect to the head by sensing the size of the corneoretinal potential with surface recording electrodes attached to the outer canthi (horizontal) and above and below one eye (vertical). The two major advantages of the EOG are that the recording electrodes are easy to apply and that the technique does not require the head to be stabilized in order to record eye position with respect to the head. One disadvantage is that removal of the electrodes can be uncomfortable, and the adhesives can produce minor skin irritation. Other disadvantages are that the corneoretinal potential drifts unpredictably in some subjects and varies with the ambient light level (Gonshor and Malcolm, 1971). Also, the EOG electrodes record potentials from muscles in their vicinity which may be activated during blinks or facial movements. Nevertheless, with a careful application of the

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electrodes, a constant level of ambient illumination and cooperative relaxed adults, the EOG consistently has a horizontal, linear range of at least ± 30 deg and a resolution of 1 deg (Young and Sheena, 1975).

Corneal reflection. In most corneal reflection systems, an infrared light beam invisible to the subject is reflected from the cornea and captured by a 2-dimensional photosensitive sheet or by a camera that superimposes the reflected beam over an image of the subject's eye. The latter technique, which estimates the direction of gaze from the relative locations of the subject's pupil and the corneal reflection, is the one most often used with infants (Hainline, 1981a, b; Harris *et al.*, 1981; Abramov and Harris, 1984; Harris *et al.*, 1984). With cooperative adults, it has a linear range of ± 12 to 15 deg and a resolution of 0.5 deg (Young and Sheena, 1975). A major limitation is that the permissible head movement is restricted by the field of view of the camera lens (e.g. the lens used by Hainline (1981a, b) allows the head to move only by ± 2 cm in any direction). Also, many corneal reflection techniques use television cameras which do not sample eye position rapidly enough to allow an accurate determination of high velocity eye movements such as saccades (Harris *et al.*, 1984). Finally, Hainline *et al.* (1984a, b) routinely exclude eye movements smaller than 2 deg from analysis because they are frequently associated with artifacts. Consequently, it appears that current corneal reflection methods are no better than carefully controlled EOG recordings.

Calibration techniques

In the most common calibration technique, an infant is presented a small light spot which is moved rapidly from one position to another in the visual field (Aslin and Salapatek, 1975; Ornitz *et al.*, 1979, 1985; Salapatek *et al.*, 1980; Aslin, 1981). If the infant makes rapid eye movements in the appropriate direction shortly (within 1 sec) after the target jumps and if the movements are nearly equal in size, it is assumed that the child is following and ultimately fixating the target. If the size of the movements varies by no more than 10% (2 deg in a 20 deg target jump), it is assumed that a reasonable calibration has been obtained. Because the amplitude of the eye movements obtained during such calibrations is often quite reproducible for cooperative infants, it has been assumed that most infants fixate with the same retinal locus

each time; this retinal locus, however, may not necessarily be the center of the fovea. The choice of the retinal locus used for fixation may also be more variable in some infants than in others (see Harris *et al.*, 1981, for a discussion).

To calibrate their infrared corneal reflection transducer, Harris *et al.* (1981) present infants with a circular array of up to nine calibration lights, 1 deg in diameter. On each calibration trial, one light is flickered, and when the experimenter judges that the subject is fixating that light, the subject's eye position is recorded for 10 sec. A computer program then calculates the average fixation position during each 10-sec trial. The error between the average fixation position and each data point is expressed as an error vector; these error vectors are then used, by means of standard least squares techniques, to calculate a 2-dimensional polynomial which maps the experimental data onto the average fixation position (see Harris *et al.*, 1981, for details). Unfortunately, a complete calibration requires the calculation of a polynomial for each calibration target, and most infants will not cooperate throughout an entire calibration procedure. Consequently, in most experiments, the calibration coefficients used are averages for all calibrated infant and adult observers who participated in the experiment (Hainline *et al.*, 1984a, b). Even when this average observer setting is used, however, calibration errors vary widely from subject to subject and may be as much as ± 3 deg even for cooperative adults (Hainline, 1981a). The errors are, if anything, worse in infants; Hainline and Lemerise (1985) assume errors of ± 3 –4 deg. Therefore, this calibration procedure apparently represents no great improvement over the calibration procedures that are already being used for EOG recordings. Indeed, Hainline and her collaborators themselves conclude that the eye movement parameters determined with their system are best regarded as relative measures within the same subjects across experimental conditions (Hainline *et al.*, 1984a, b).

Another method of calibrating eye movement recordings in infants involves introducing a prism before a fixating eye to produce an image jump and measuring the resultant eye movement (Metz, 1984). By knowing the strength of the prism and the distance of the fixation target, the resultant eye movement could be used for calibration. Although the method apparently has been tested successfully on infants (Metz, 1984), it has not found wide use in infant

research to date, possibly because this method, like others, still relies on an observer's judgment of the infant's initial fixation position and further assumes that the infant refixates the same point on the fixation target after application of the prism.

Recently, Finocchio *et al.* (1987) have developed a calibration technique which compares the experimenter's estimation of the child's fixation position, as assessed by corneal reflection, with the simultaneously measured EOG potential. A bright 1.7 deg pen light is slowly slid on a track before the child to attract its attention. When the light is stopped at known horizontal angles, an observer, who slides with the target, sights along it to estimate and record when the corneal reflection is in the same position with respect to the pupil as it was when the infant fixated centrally. The sliding spot coupled with the sliding, talkative observer apparently is seductive to many infants. Finocchio *et al.* (1987) have reported that the amplitude of the eye movements recorded using this technique varies within ± 1.5 deg for targets placed at ± 15 deg for 2- and 3-month old infants.

In summary, although EOG is sometimes regarded as an outdated method for recording eye movements, we feel it is the method of choice for many studies of infant eye movements. In particular, the EOG *must* be used for studies of the vestibulo-ocular reflex, in which subjects are oscillated or rotated, and studies of the optokinetic response to full field stimuli, in which the visual field must be free of distracting stimuli like cameras and mirrors (see below). Also, experiments that require subjects to use their entire oculomotor range are better suited to the EOG, which has a larger linear operating range. On the other hand, corneal reflection systems can be used in situations in which the stimulus field is small and fixed in space, as when measuring eye movements than scan a restricted visual scene, such as a T.V. monitor. Under these conditions, corneal reflection systems, when properly calibrated, will specify the absolute position of gaze more accurately and will detect smaller eye movements than the EOG. However, corneal reflection systems are both more expensive and require more careful alignment of the subject's head than EOG systems. Thus, despite its disadvantages, which include contamination by muscle potentials, possible drifts and gain changes, and slightly lower sensitivity, the EOG is probably prefera-

ble to corneal reflection systems in most experimental situations involving human infants.

Further considerations

The study of oculomotor behavior in infants is also complicated by a variety of problems unrelated to the difficulty of producing calibrated eye movement recordings. Possibly because their eye movements are not well developed, infants are somewhat more likely to move their heads to pursue or refixate visual targets than are adults (Regal *et al.*, 1983; Roucoux *et al.*, 1983). As a result, most studies require some sort of head restraint, involving either an adult who holds the baby firmly (e.g. Hainline *et al.*, 1984a, b) or a seat in which the baby sits or lies with his head restrained by padding (e.g. Aslin and Salapatek, 1975; Ornitz *et al.*, 1979, 1985; Salapatek *et al.*, 1980; Aslin, 1981). Some infants simply do not tolerate such restraint. Babies are also subject to unpredictable, spontaneous changes in behavioral state; they become fussy or fall asleep. Therefore, the researcher often must choose between drawing conclusions from a small amount of usable data gathered from each of a large number of infants, or from a large amount of data gathered from a few very cooperative infants. The labile alertness of infants places a premium on finding the most seductive stimuli. Since these are rarely similar to those used in studies of adult oculomotor behavior and also often vary from one infant lab to another, comparisons across studies become problematic. Finally, as others have repeatedly pointed out, if infant eye movements are "less mature" than those of adults, this result may be due, in part, to sensory immaturity rather than motor immaturity (Aslin, 1981; Hainline, 1985). Infants are sensitive to different ranges of stimulus parameters than are adults, and these ranges change as the infant develops. Therefore, oculomotor experimenters must choose stimuli that are readily discernible by infants of that age (see Boothe *et al.*, 1985, for a review). In view of all these difficulties, it is tempting to conclude that only the brilliant or the foolish undertake studies of oculomotor behavior in human infants.

TYPES OF EYE MOVEMENT

Vestibulo-ocular reflex

Whenever the head is moved there is a potential for the image of the world to move across the retina, thereby resulting in a functional loss

of vision due to blur. To reduce the slip of the visual world across the retina, compensatory reflexive eye movements have evolved to help stabilize retinal images during head motion. These compensatory eye movements are called the vestibulo-ocular reflex (VOR) since the afferent signal that generates them originates in the head movement sensors of the vestibular apparatus (see Fuchs, 1981, for a review).

Adults. The operation of the VOR is usually evaluated for passive, rather than active, head movements by placing subjects in a rotatable chair. In most adult and all infant studies, subjects are rotated about a vertical axis only (i.e. yaw rotation); thus, only the horizontal VOR is tested. The kinds of rotation employed are either sinusoidal oscillation or unidirectional accelerations to or from a constant velocity.

Figure 1(A) shows schematically that sinusoidal head rotations in one direction produce slow eye movements in the opposite direction. The slow compensatory eye movements are periodically interrupted by rapid movements in the direction of head rotation, producing a sawtooth pattern known as *vestibular nystagmus*. The efficacy of the slow compensatory movement is assessed by differentiating eye position (E) to produce eye velocity (\dot{E}). This strategy allows the rapid component to be ignored, so that the ratio of the resultant compensatory eye velocity to the imposed head velocity, i.e. the GAIN, $G = \dot{E}/\dot{H}$, can be calculated. At some frequencies of oscillation, the compensatory eye movements may not be exactly out of phase with head velocity; therefore, the phase shift of peak eye relative to peak head velocity [Fig. 1(A)] is also measured.

In adults, the gain and phase of the VOR depend on several factors. First, the gain of the VOR must be measured in complete darkness, since the presence of visual stimuli can cause facilitation (if the visual stimuli are stationary in space) or suppression (if the stimuli rotate with the subject) of VOR gain (see Fuchs, 1981, for a review). Indeed, adults can change the VOR gain simply by fixating an *imaginary* target that is stationary in space or rotating with them (Barr *et al.*, 1976; Baloh *et al.*, 1984). Second, changes in alertness and attention can cause changes of VOR gain (Collins, 1974). Finally, the VOR gain and phase are dependent on the frequency of head rotation. Over the frequency range usually considered typical of human head movements (about 0.2–1.5 Hz), the VOR of the

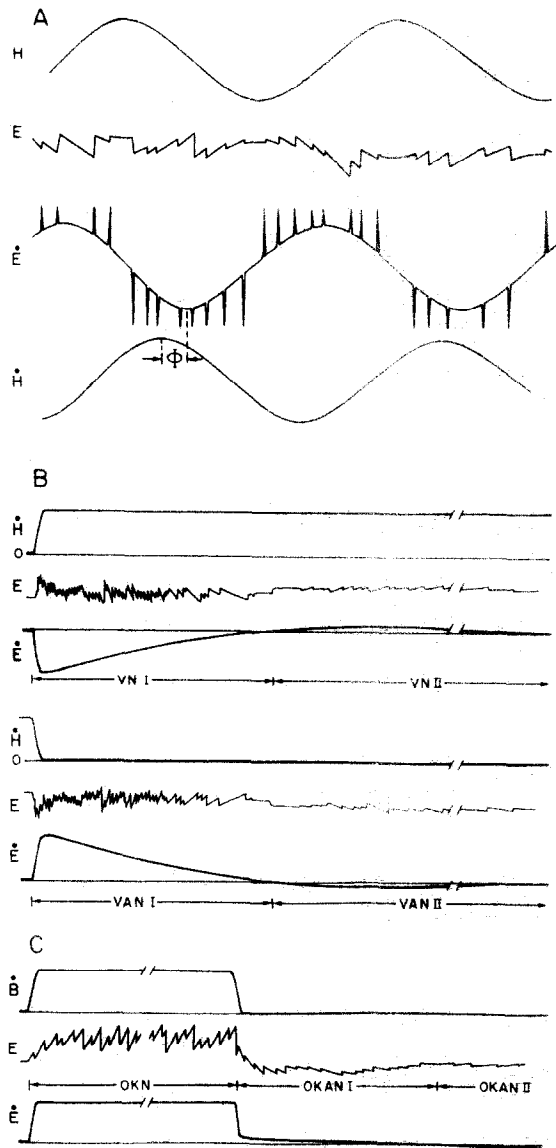


Fig. 1. Schematic illustrations of vestibular and optokinetic eye movements in man. In (A), a sinusoidal head rotation in the dark (H) elicits compensatory nystagmic eye movements (E) which are best seen by comparing head (\dot{H}) and eye (\dot{E}) velocities. In (B), unidirectional head rotation at constant velocity (\dot{H}) elicits nystagmic eye movements whose slow-phase velocity (\dot{E}) has two components (VN I and VN II). Stopping the head causes an oppositely directed afternystagmus whose velocity has a similar time course (VAN I and VAN II). In (C), unidirectional rotation of the whole visual field (\dot{B}) elicits nystagmic following movements (OKN) which, when the lights are extinguished (i.e. \dot{B} drops to zero), persists as two components (OKAN I and OKAN II). See text for more details.

alert adult subject in the dark has a gain of about 0.6–0.8 and approximately zero phase shift [as measured in Fig. 1(A)].

Figure 1(B) shows the eye movement re-

sponses that result when a subject is rapidly accelerated from rest to a constant angular velocity. Once again, this rotary stimulus produces a nystagmic eye movement pattern with a slow phase opposite in direction to the chair movement. After a constant chair speed has been reached, the velocity of the slow phase decreases exponentially; its total duration is 20–30 sec. Thereafter, a nystagmus of much reduced amplitude in the opposite direction sometimes appears; it lasts between 1 and 2 min (see Robinson, 1981, for a discussion of VOR time constants). The first and second nystagmus patterns during head rotation are called primary and secondary *perrotatory nystagmus*, respectively. When the head is rapidly decelerated to rest, a primary and secondary *postrotatory nystagmus* with time-courses similar to those of perrotatory nystagmus results [Fig. 1(B)]. The time course of nystagmus is thought to be due to a peripheral transduction process with a short time constant and central neural processes with longer time constants (Robinson, 1981).

Infants. Because accurate measurements of the VOR require that the subject remain alert in complete darkness, VOR data are particularly difficult to obtain from infants (see Ornitz, 1983, for an extensive review). Information about the time course of the nystagmus is easiest to obtain, since the eye movement transducer need not be calibrated to reveal the existence and duration of vestibular nystagmus. Ornitz and colleagues (Ornitz *et al.*, 1985) find that the time constant of primary *perrotatory nystagmus* in the 5-month-old is about 7.5 sec, compared with about 10.5 sec in their adults; the greatest increase in the time constant occurs between the 5 and 10th month. The time-constant is even shorter (less than 1 sec) in newborns (5 days old) (Weissman *et al.*, 1986). The total duration of perrotatory nystagmus is also short in neonates and undergoes its greatest increase within the first year of life (Kaga *et al.*, 1981). The duration of secondary perrotatory nystagmus is also less in infants under 1 year of age than in adults (Ornitz *et al.*, 1979). Finally, the total duration of both primary and secondary *postrotatory nystagmus* apparently is less in infants under one year of age than in adults (Cordero *et al.*, 1983), although a later study by these same authors appears to contradict their previous findings on primary postrotatory nystagmus (Clark *et al.*, 1984). It has been suggested that this shortening of the per- or postrotatory time-courses in infants reflects an immaturity primar-

ily in central vestibular mechanisms (Clark *et al.*, 1984; Ornitz *et al.*, 1985).

Most studies documenting changes in VOR gain with age use some measure of the average or peak velocity obtained during the nystagmus caused by accelerations to, or decelerations from, constant velocity stimuli. Although neither of these measures allows the absolute VOR gain to be determined, each provides an index of the efficacy of the VOR which may be compared in infants and adults under identical stimulus conditions. Such comparisons indicate that infants 5–10 months old attain higher VOR velocities during primary perrotatory nystagmus than do adults, although the data show considerable scatter (Ornitz *et al.*, 1985, Fig. 4). Similarly, the velocity of primary and secondary afternystagmus is higher in infants less than one year of age than in adults (Cordero *et al.*, 1983, Fig. 2). These data suggest that the VOR gain in infants is higher than in adults. This suggestion recently has been confirmed by Finocchio *et al.* (1987), who measured the compensatory eye movements that result from applying brief velocity pulses of yaw rotation in the dark. The average VOR gain 2- and 3-month-old infants was approximately 1, more than 50% greater than that obtained under similar conditions in young adults where the gain was only 0.6. Anecdotal data reported by Regal *et al.* (1983) also indicate that the gain of 1- and 3-month-old infants is close to one (see their Fig. 2). Recently, VOR gains of at least 0.9 also have been reported in infants under 1 year of age for both velocity pulses and sinusoidal oscillations (Ornitz and Honrubia, 1987). Finally, children as old as 16 years of age still have an elevated VOR gain, indicating that the VOR takes a long time to reach adult values (Herman *et al.*, 1982).

In summary, the existing data are consistent with the view that the various time constants describing the human VOR are shorter at birth than in adulthood. Within the first 3–5 months of life, they undergo a dramatic increase to nearly adult values. The gain of the VOR, on the other hand, is larger in infancy and declines to adult values over a very long time-course that may extend into the teenage years.

The optokinetic response

Adults. Because the gain of the adult VOR is less than 1, head rotations made in a well-lit environment would tend to produce some movement of the entire visual world in the

opposite direction. However, these visual image motions cause visually generated eye movements in the same direction, called the optokinetic response (OKR) (see Cohen *et al.*, 1981, for a review). When combined with the VOR, the OKR produces good stabilization of the visual world on the retina.

Although full field motion of the visual world occurs naturally only during head movement, it can be simulated by placing a stationary subject at the center of a textured, rotating drum. Under these circumstances, the subject exhibits optokinetic nystagmus (OKN), in which the eyes are drawn along at the velocity of the visual stimulus (slow phases), and are periodically reset in the opposite direction by saccades (fast phases). Figure 1(C) shows a schematic pattern of optokinetic eye movements generated by a moving visual scene. In adult humans instructed to stare passively but attentively at optokinetic stimuli, the slow phase velocity jumps rapidly to almost 90% of the stimulus velocity for motions of 30 deg/sec or less, and is maintained as long as the stimulus motion continues. If the observer is suddenly plunged into darkness, the slow phase velocity first drops precipitously by at least 70%, but the nystagmus nevertheless persists for some time in darkness. The velocity of this nystagmus, called primary optokinetic afternystagmus (OKAN I), can be as high as 15 deg/sec for higher OKN velocities, decays exponentially with time and lasts about 45–50 sec (Cohen *et al.*, 1981). If the optokinetic stimulation is long in duration (about 4 min), the OKAN will reverse in direction [Fig. 1(C), OKAN II]. Optokinetic afternystagmus thus resembles the afternystagmus generated by the termination of a vestibular stimulus [Fig. 1(B)].

For human adults, the OKN slow phase velocity elicited with both eyes open is approximately equal for stimuli moving to the left or right. Stimuli observed monocularly also produce similar slow phase velocities for both directions of motion. In lower mammals such as rabbits, however, monocular OKN is directionally asymmetric, with temporal to nasal (T–N) stimulus motion in either eye eliciting a more vigorous response. If animals such as cats, which normally show a symmetrical monocular OKN, are reared under conditions of monocular deprivation or surgically induced strabismus, they also will show an asymmetrical monocular OKN (Van Hof-van Duin, 1976, 1978; Malach *et al.*, 1981, 1984). These procedures also prevent the development of cortical

binocularity (see Movshon and van Sluyters, 1981, for a review). Since it has been shown that the cortical input to the brainstem structures thought to control OKN in cats is binocular (see Hoffmann, 1983 for a review), it has been suggested that the presence of an OKN asymmetry in human infants may reflect the slow maturation of cortical binocularity (Atkinson and Braddick, 1981; Naegle and Held, 1982, 1983). Furthermore, animals with an asymmetric monocular OKN also display a slow initial increase in OKN eye velocity rather than the immediate fast rise seen in humans and monkeys (Cohen *et al.*, 1977, 1981). It is thought that the initial rapid rise actually represents a voluntary smooth pursuit of the stimulus, an eye movement that is much better developed in the foveate primate. The subsequent slower rise of eye velocity to match that of the target is thought to reflect an optokinetic following reflex.

Infants. As with vestibular experiments, virtually every study of OKN in human infants is restricted to horizontal stimuli. Large, patterned, horizontally moving visual stimuli readily elicit a symmetric binocular OKN from alert infants, including newborns (Kremenitzer *et al.*, 1979; Schor *et al.*, 1983). Monocular OKN, however, is noticeably asymmetric and most of the recent studies have concentrated on the development of a symmetrical monocular OKN. Atkinson and Braddick (1981), who simply observed the OKN and timed its duration using stopwatches, concluded that monocular OKN was asymmetric in 4- and 8-week-old infants, but approximately symmetric in 12-week-olds; specifically T–N stimulus motion elicited longer periods of following than N–T motion for either eye. Similar findings have been reported by Smith *et al.* (1987). The presence of these horizontal OKN asymmetries was confirmed by Naegle and Held (1982, 1983), who used an uncalibrated EOG to determine the cumulative eye displacement produced during 25 sec trials. The slopes of these cumulative displacement curves provide a relative (i.e., uncalibrated) measure of eye velocity. At 8 weeks, the T–N slope was approximately 3 times the N–T slope. The directional asymmetry gradually decreased over the next several weeks so that by the 20th to 25th weeks of age, the OKN was symmetrical. Unfortunately, it cannot be determined from these studies whether the magnitude of the optokinetic gain also had reached adult values. If the OKN gain of infants is low,

however, the high neonatal VOR gain noted earlier might facilitate stabilization until the OKR can develop fully.

It is unclear whether the development of a symmetrical OKN can be accelerated by visual experience. Van Hof-van Duin and Mohn (1984a, b, 1985, 1986, 1987) report that 130 premature infants whose ages were corrected for 40 weeks of gestation developed a symmetrical OKN at the same post-term age (about 26 weeks) as full term infants tested in the same apparatus. On the other hand, Roy *et al.* (1987) found that 25 premature and full term infants all developed a symmetrical OKN by 20–25 weeks after birth regardless of gestational age.

Monocular optokinetic after-nystagmus, like OKN, also is immature at birth. Although binocular stimulation produces a symmetrical OKAN I and OKAN II, either temporalward or nasalward monocular OKN is always followed by a nasalward OKAN I. By 18 weeks of age, 50% of the infants showed some N–T OKAN I and by 24 weeks essentially all showed a symmetrical OKAN I; the greatest development of monocular OKAN occurs between the 3rd and 6th months (Schor *et al.*, 1983).

In summary, even infants less than 1 month old exhibit a symmetrical OKN and OKAN if the drum is viewed binocularly. If the drum is viewed monocularly, T–N OKN is always more robust than N–T. Also a N–T OKAN I cannot be generated for any direction of drum movement. The N–T components of OKN and OKAN develop gradually and are similar to the T–N components by about the 24th week of life. Although monocular OKN becomes symmetrical over the first 6 months of life, it is unclear whether the neonatal OKN gain is higher or lower than that of adults and whether it matures over the same time interval.

Because the directional asymmetries in horizontal OKN seen in young infants are similar to those found in animals that have undergone monocular deprivation or surgically induced strabismus, procedures that prevent the normal development of cortical binocularity, it has been hypothesized that the development of a symmetrical OKN is related to the development of binocularly driven cells in visual cortex. Normal human infants develop stereopsis, which also depends on cortical binocularity, between 20 and 30 weeks of age (see Boothe *et al.*, 1985, for a review). Moreover, infants deprived of binocular vision by strabismus or unilateral cataracts from birth fail to develop either stereopsis or a

symmetrical monocular OKN (Atkinson and Braddick, 1981; Naegele and Held, 1983; but also see Braddick and Atkinson, 1983). In fact, if a unilateral cataract occurs at any time up to 18 months of age, an asymmetrical OKN will result (Maurer *et al.*, 1983 and in press; Lewis *et al.*, 1985, 1986).

In addition to binocularity, however, other visual capacities that could contribute to OKN are immature in young infants. For example, the central retina, thought to be the primary source of retinal motion information for pursuit eye movements and the fast rise of OKN velocity (Baloh *et al.*, 1980; Ohmi *et al.*, 1986; van Die and Collewyn, 1986) undergoes developmental changes until approximately the 20th week of life in human infants (Abramov *et al.*, 1982). Also, the T–N predominance of OKAN may be due to inadequate direction selectivity in cortical pathways that provide information about retinal image motion to brainstem structures (Schor *et al.*, 1983).

The ease with which OKN can be elicited from even very young infants has led many researchers to use OKN as a measure of visual performance, and especially acuity. In most early studies, infants were presented with various large moving visual scenes, each containing pattern elements of different sizes (see Dobson and Teller, 1978, and Banks and Salapatek, 1981, for reviews and critiques of these studies). If a stimulus failed to elicit following eye movements, it was assumed that the pattern elements were too small for the infant to resolve.

Because a systematic variation of pattern parameters is difficult to achieve for very large stimulus areas, however, more recent studies have taken advantage of the flexibility in stimulus control offered by cathode ray tube (CRT) displays. Although such small field stimuli are less effective at eliciting the OKR (Schor and Narayan, 1981), both infants and adults exhibit OKN-like eye movements when watching pattern elements move in one direction across the face of a CRT. Atkinson and Braddick (1981) showed that a 0.19 c/deg, high contrast vertical stripe pattern moving across a CRT (subtending 62 deg by 62 deg) at 12 deg/sec produces the same monocular OKN asymmetry in 1- and 2-month-olds as is generated by full-field stimulation. Hainline *et al.* (1984a) showed that a 0.3 c/deg high contrast vertical grating moving across a CRT subtending 30 deg by 22 deg at 7 deg/sec produces a binocular OKN to both horizontal and vertical directions of pattern

movement in infants of 3–16 weeks of age. Infants under 16 weeks of age showed slower OKN to downward stimulus motion, an asymmetry which has sometimes been reported in adult animals and humans (see Hainline *et al.*, 1984a, for a discussion). A problem with small field stimuli, however, is that they may elicit primarily foveal smooth pursuit movements, such as those described in the following section.

Smooth pursuit

Adult. If the entire visual world moves, the OKR serves to stabilize its image over the whole retina. More often, however, only a small part of the visual world moves and, to examine the small visual target, eye movements must place it not just anywhere on the retina but on the fovea, where acuity is highest. If a moving object of interest appears, the eyes first execute a rapid movement (a saccade) to “foveate” the object and then slow eye movements, called *smooth pursuit*, to keep the object on the fovea. The fast increase in slow phase velocity when an optokinetic drum is rotated and the rapid decrease when it stops is believed to reflect such a smooth pursuit response (see Lisberger *et al.*, 1987, for a review).

Smooth pursuit is usually evaluated by requiring a subject with head fixed to track a small target moving over a homogeneous or dark background. Most studies have examined horizontal eye movements elicited either by ramp (unidirectional, constant velocity) or sinusoidal target motions. Using either stimulus, smooth pursuit is extremely good for stimuli reaching peak velocities of 30 deg/sec or less; at higher stimulus velocities, tracking becomes increasingly more saccadic. When adults are first exposed to sinusoidal target motions, their eyes lag behind the target with a phase shift that increases with the frequency of the oscillations. With no specific instructions, however, adults soon reduce their phase lags so that over the frequency range 0.3 to about 0.8 Hz, their eyes move essentially in phase with, or even lead, the target (Lisberger *et al.*, 1981, and others). Periodic target motions, then, have been used to test for the presence of predictive tracking.

Infants. Most alert newborns will follow interesting moving objects with some combination of head and eye movements. If the head is held, the eyes appear to track by making a series of saccades. There is some controversy, however, about whether any smooth pursuit exists between the saccades in very young infants. Krem-

initzer *et al.* (1979), using a 12 deg solid black circle moving at different velocities between 9 and 40 deg/sec, claim that the majority of their eye movement records in neonates show at least some smooth pursuit segments; however, pursuit makes up only 15% of the tracking movement and no smooth pursuit at all occurs for targets moving faster than 32 deg/sec. On the other hand, Aslin (1981), using a black bar 2 deg wide by 8 deg high moving sinusoidally at peak velocities from 10–40 deg/sec, found that, until the ages to 5 to 6 weeks, infants tracked the target using saccades exclusively. Perhaps the discrepancy in smooth pursuit performance is due to the fact that the larger stimulus used by Kreminitzer *et al.* elicits an optokinetic response (see Atkinson and Braddick, 1981, for a discussion of this issue). This appears to be possible since Shea and Aslin (1984) showed that under similar conditions a 6 deg target elicits smooth pursuit eye movements at an earlier age than a 2 deg target.

After they have appeared at about the 6th week of life, smooth pursuit movements to small targets undergo a gradual increase in peak velocity over the next several weeks (Aslin, 1981; Shea and Aslin, 1984). It is unclear, however, at what age a fully mature smooth pursuit response is present; Shea and Aslin (1984) report that pursuit gain is still improving at 8 months of age. Like smooth pursuit gain, the ability to track predictively also appears to improve with age. At least some infants as young as 10 weeks old, but not younger, seem to track nearly in phase with some cycles of a sinusoidal target, and the error between target and eye position appears to decrease after the child has tracked a number of similar cycles (Aslin, 1981; Fig. 6). Shea and Aslin (1984) also showed that for infants up to 8 months of age, smooth pursuit is more accurate for sinusoidal target oscillations than for trapezoid (i.e. ramp and hold) target trajectories.

If the head is free to rotate, Roucoux *et al.* (1983) show that infants as young as 1 month old track slowly moving comic characters with smooth head movements and a combination of saccadic and smooth pursuit eye movements. Unfortunately, only one very low gain record is presented to substantiate the existence of smooth pursuit and the size of the target is not indicated. The largest stimulus used in their experiment, however, is comparable to that used by Kreminitzer *et al.* (1979). Another record in Roucoux *et al.* (1983) suggests that smooth

pursuit has improved considerably by 4 months of age.

In summary, it appears that the presence of smooth pursuit in young infants depends upon the size and speed of the tracking target. Even newborns appear to make smooth eye movements to large, slowly-moving objects. Unfortunately, it seems likely that smooth following of a large spot by very young infants may reflect, in part, an activation of the OKR. Smooth pursuit ability obviously improves with age, but it remains unclear at what point in development smooth pursuit becomes adultlike over a large range of target sizes and velocities.

Saccades

Adults. Saccades, which are the fastest of all eye movements, serve to rapidly redirect the position of the eyes to fixate different objects in the visual world. In adults, controlled saccades are elicited by rapid jumps of a small target spot from a central to an eccentric position. Most adults make a single accurate saccade to targets at eccentricities of 15 deg or less. For larger target eccentricities, the saccade usually travels only about 90% of the distance to the target and thus a second, and on rare occasions a third, corrective saccade is required. *Hypometria*, then, is common for large eccentricities but uncommon for small eccentricities; *hypermetria* is an infrequent occurrence in normal adults (Fuchs, 1971).

An adult saccade is usually well characterized by its duration and peak velocity. Saccade duration increases linearly with saccade size at a rate of about 2 msec/deg for saccades ranging from about 3 to 30 deg (Fuchs, 1971). Saccadic peak velocity also increases roughly linearly with size until about 15 deg, whereupon the peak velocity gradually shows a lesser increase with size and eventually saturates at about 600–700 deg/sec.

Although many investigators consider that the saccade is a ballistic movement whose duration–amplitude and peak velocity–amplitude relations are pretty consistent from adult to adult, some studies point out that there is considerable variability between the data of normal alert subjects (Schmidt *et al.*, 1979). Furthermore, it is well known that inattention slows saccades. A horizontal saccade can also appear to be slow if it is the horizontal component of an oblique saccade with a large vertical component since, in that situation, the smaller component is stretched in duration. The

parameters of saccades also can be affected if they are executed during head rotations. These last several points illustrate that a comparison between adult and infant data may be difficult. Not only is the alertness of infants highly variable, but oblique saccades may be misinterpreted as purely horizontal if the infant's vertical eye position is not monitored. Finally, absolute head stabilization is rarely obtained in infants.

Infants. If a central spot jumps to eccentric locations of up to 40 deg horizontally (Aslin and Salapatek, 1975; Salapatek *et al.*, 1980), infants as young as 1 month of age reliably make a saccade in the correct direction; however, they are most reliable if the target jumps to within 10 deg of the initial direction of gaze. Infants also respond to nearby targets at shorter latencies, but these latencies are still considerably longer than those of adults. In 1- and 2-month-olds, most saccadic responses to eccentric targets are hypometric, especially for eccentricities of greater than 20 deg; therefore, several successive saccades are required. All of the successive saccades, which may number up to 5, appear to be roughly of the same size (Aslin and Salapatek, 1975; Salapatek *et al.*, 1980). For 10 deg eccentricities, single saccades occur about half the time.

Infants who are permitted to move their heads also make a series of successive hypometric saccades (Roucoux *et al.*, 1983). Again, more saccades are made to the more eccentric targets. The number of successive saccades decreases with age, as does the latency of the first saccade (Regal *et al.*, 1983), but it is unclear when the size, number and latency of saccades to eccentric targets reach adult values.

In contrast to these findings, however, no evidence of hypometric saccades is seen if infants simply scan visual patterns freely (Hainline *et al.*, 1984b). If the patterns consist of textures (i.e. line gradients and different size checkerboards), Hainline *et al.* (1984b) conclude that 1-month-old infants and adults have similar peak velocity vs amplitude relations for saccades. When the same infants view patterns of different geometrical forms, however, the same relation has a lower slope (i.e. saccades are slower). The conclusion of Hainline *et al.* (1984b) that scanning saccades of infants under some conditions are adult-like should be confirmed by further experiments, since their eye movement measurements were not individually calibrated, their infant data frequently was

composed of as few as 10 saccades per subject, and their data contained an unknown number of oblique saccades which have unusual characteristics. Also, Hainline *et al.* (1984b) report that during attempts at fixation, infants sometimes exhibit fast oscillations whose half cycles have the characteristics of back-to-back saccades. This eye movement pattern has never been observed in adults.

In summary, it seems premature to conclude that the saccades of very young infants, especially those to small targets, are completely adultlike. As is the case with smooth pursuit eye movements, some stimulus conditions may elicit more or less adultlike eye movements. As Hainline *et al.* (1984b) point out, however, it cannot be determined whether the infants merely find free scanning of large textured scenes a more interesting task than tracking a small object against a dark background. Finally, although older infants appear to show more adultlike saccades, the age at which the saccadic eye movement system is fully developed remains to be determined.

CONCLUSIONS

Virtually all of the studies described in this review conclude that the eye movements of young infants differ in some way from those of adults. As both Aslin (1981) and Hainline (1985) have indicated, however, an immaturity or absence of movements does not necessarily indicate that the oculomotor system undergoes development early in life. Failure on the part of an infant to move his eyes in response to motion of a visual target may also mean that the infant has failed to see the target, or that the infant can see the target but cannot accurately determine its location or velocity. Because the motivational state of an infant is largely beyond the control of the experimenter, it may simply mean that the infant is not interested in moving his eyes.

Compounding these problems is the difficulty of reconciling the sometimes discrepant findings of apparently similar studies carried out in different laboratories. For example, the criteria for judging infant alertness are usually vague. Many studies omit samples of raw eye movement recordings, so that it is difficult to judge the quality of the data. The conclusions of other studies appear to be based on a handful of records from a few infants. Also experimental paradigms differ, and we have seen that stimulus

parameters such as target size are apparently critical in determining whether a movement (e.g. smooth pursuit) will or will not occur. In some studies, the same infants are tested at different ages to provide longitudinal information about developmental changes; in others, groups of infants at different ages are tested in single sessions. Finally, some experimenters choose to regard the best (most adultlike) performance of any infant at a given age as representative of all the infants at that age, whereas others present findings in terms of the average performance of the group.

Despite the problems in interpretation and methodology, the studies of infant oculomotor development should yield valuable insights into how the various eye movement types and their symbiotic interactions develop. In our opinion, however, we have learned all we can from qualitative studies. What is now required are studies with carefully calibrated eye movements. While this is admittedly very difficult, only such quantitative studies will allow us to answer not just whether neonates display a type of eye movement, but how good it is. Then we will perhaps be able to determine whether eye movements exist to help the developing visual system or vice versa.

Acknowledgements—The support of grants RR00166 and EY00745 (A.F.F.) and NS19222 and NS12661 (C.L.S.) during the writing of this review is gratefully acknowledged. We also thank Davida Teller and Han Collewyn for their comments on the manuscript. Finally, we are grateful for the word processing skills of David Lovell and the bibliographic assistance of Susan Usher.

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