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Smooth Pursuit in 1- to 4-month-old Human Infants

JAMES O. PHILLIPS,*†‡§ DOM V. FINOCCHIO,*† LUAN ONG,* ALBERT F. FUCHS*†‡

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The ability of human infants ≤4 months of age to pursue objects smoothly with their eyes was assessed by presenting small target spots moving with hold–ramp–hold trajectories at ramp velocities of 4–32 deg/sec. Infants as young as 1 month old followed such target motions with a combination of smooth-pursuit and saccadic eye movements interrupted occasionally by periods when the eyes remained stationary. The slowest targets produced variable performance, but targets moving 8–32 deg/sec produced consistent pursuit behavior, even in the youngest infants. By the fourth month, eye-movement latency decreased and smooth-pursuit gain and the percentage of smooth pursuit per trial increased for all target velocities, though these measures had not yet reached adult levels. © 1997 Elsevier Science Ltd

Infant Oculomotor Smooth pursuit EOG Saccades

INTRODUCTION

Human visual development requires a complex interaction between evolving sensory and motor processes. The sensory system needs stable and coherent visual images to develop fully, while the oculomotor system must rely on the developing visual system to guide the acquisition and fixation of objects in the visual world. While much is known about the development of visual perception, the co-development of the oculomotor system is poorly understood. A case in point is the development of the smooth-pursuit eye movements by which we follow slowly moving objects.

Adults can accurately pursue objects moving at speeds of >30 deg/sec (Rashbass, 1961; Young, 1962; Robinson, 1965). When an object at rest begins to move at a constant velocity, the eye begins to move after approx. 130 msec, sliding in the direction of object motion. The eye velocities achieved during the slide invariably are less than that of the target, and a position error results from the 130-msec delay, so a "catch-up" saccade in the direction of target motion is required. Such saccades usually bring the eyes on target, whereupon they continue to move at approximately the target velocity. Any residual difference between target and eye position is eliminated by additional catch-up saccades. If the moving target suddenly stops, the eye continues its smooth pursuit for ~100 msec before it decelerates and eventually stops. When the smooth motion of objects is predictable, adult smooth-pursuit performance improves. For example, if the direction, speed, and time of occurrence of a hold, ramp, and hold target motion are known in advance, subjects learn to anticipate target movement, thereby reducing or even eliminating the delay before the eye-movements response. In contrast, young human infants are said to have difficulty following either random or predictable smooth target movements with smooth eye movements, although they seem able to attend to and move their eyes toward such moving objects.

There is considerable disagreement as to the efficacy of infant smooth pursuit. Some authors have suggested that very young (1- to 2-month-old) infants make smooth eye movements in response to smoothly moving targets (Kremenitzer *et al.*, 1979; Roucoux *et al.*, 1983), whereas others have reported that such infants track smoothly moving targets only with rapid (saccadic) eye movements (McGinnis, 1930; Dayton & Jones, 1964; Dayton *et al.*, 1964; Aslin, 1981; Bloch & Carchon, 1992). In addition, it is unknown whether the smooth eye movements observed even in older infants show the parametric relations between eye and target velocity characteristic of adult smooth pursuit (Shea & Aslin, 1990). Whether such infants are capable of predictive eye movement is unresolved. For example, older infants whose pursuit lags behind a smoothly moving target may continue moving their lagging eyes for up to 600 msec after a step–ramp–hold target motion stops, thereby continuing to reduce the position error, but it is unclear whether this continuation of pursuit represents a prediction of the final target hold (Shea & Aslin, 1990) or simply an inability to stop eye movement. Also, 3-month-old infants can track

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Departments of *Psychology, †Physiology and Biophysics, and ‡Regional Primate Research Center, University of Washington, Seattle, WA 98195, U.S.A.

§To whom all correspondence should be addressed at the Department of Psychology, Box 351525, University of Washington, Seattle, WA 98195, U.S.A.

large, slowly moving visual stimuli with little position error (Aslin, 1981) and can produce accurately timed reversals of eye-movement direction in response to sinusoidal whole-field target motion (von Hofsten & Rosander, 1996). Both these behaviors require some form of prediction.

Interpretation of the existing infant smooth-pursuit data is further clouded by the limits of infant vision and the attendant problem of designing a compelling stimulus that consistently elicits smooth pursuit alone. Most investigators use full-field stimuli to study infant "tracking". Those that have limited the size of the stimulus have resorted to complex stimuli such as bars, or Mickey Mouse heads, which still subtend many degrees of visual arc. Such stimuli open the possibility that smooth pursuit is being augmented or inhibited by other eye movements, such as optokinetic eye movement.

Finally, there are technical difficulties associated with eye-movement experiments in human infants. Many studies have relied on indirect measures of eye-movement performance to calibrate sophisticated, often high-resolution, instruments. Second, investigators have not used a consistent definition of infant smooth-pursuit movements, making comparisons across studies difficult.

In this paper, we examine the smooth-pursuit behavior of 1- to 4-month-old human infants and compare it with that of adult control subjects in the same paradigm. To address the concerns raised above, we (1) use a small target in an otherwise completely darkened room; (2) use a simple hold–ramp–hold target motion, which allows measurement of timing and smooth-pursuit performance in response to constant velocity targets; (3) measure eye movements by our simple but carefully calibrated electro-oculographic (EOG) system; and (4) establish objective criteria for the existence and evaluation of smooth pursuit. Some of this work has appeared in abstract form (Phillips *et al.*, 1994).

METHODS

Twenty infants (6, 5, 5, and 4 at 1, 2, 3 and 4 months of age, respectively) and eight unpracticed adults were studied. Of the 20 infants, all provided useful data. Infant subjects were introduced to the laboratory environment under subdued red lighting while their parent(s) read and signed the informed consent documents and had laboratory procedures explained to them. Adult subjects were introduced to the laboratory while giving informed consent. We then placed miniature EOG electrodes (Sensormedics) just lateral to the outer canthus of each eye, and a reference electrode on the right ear lobe (Finocchio *et al.*, 1990).

The experimental setting is shown in Fig. 1. Adult subjects were seated in a chair 50 cm in front of a neutral gray stimulus panel containing a red target light (1700 mCD/m^2) which subtended 1.7 deg of visual arc. They stabilized their heads by clasping their chins while their arms rested securely on an arm rest. They were instructed to "follow the target with your eyes". Infant subjects were gently handed to an experimenter, who held them in her lap while sitting in the subject chair. The holder stabilized the infant's head by clasping it from above and below between both hands (see Fig. 1). The experimenter also restrained the infant's trunk by moving her forearms and elbows inward across the infant's stomach and chest. The infant was positioned so that its eyes were vertically level with and 50 cm from the target light at its central position. After the subjects were comfortably seated, the EOG electrodes were connected to a preamplifier, the red room lights were turned off, and the EOG was allowed to stabilize. Then, an initial calibration procedure was performed. To calibrate the EOG, the stimulus light was repeatedly moved manually from straight ahead to 10 deg right and left by a second experimenter (the hidden observer), who stood behind the stimulus screen and looked directly at the subject's eyes through a small viewing hole located above, and moving with, the target light (Fig. 1). This experimenter controlled the stimulus motion and watched the corneal reflection of the target light in the eyes of the subject. When the reflection was symmetrically placed on the cornea of each eye, the subject was considered to be accurately looking at the target, whereupon the observer activated an "on target" foot switch. A third experimenter, located in an adjacent room, monitored the EOG and provided occasional voltage offsets to compensate for drift. The EOG gain remained constant throughout the 30-min duration of an average session.

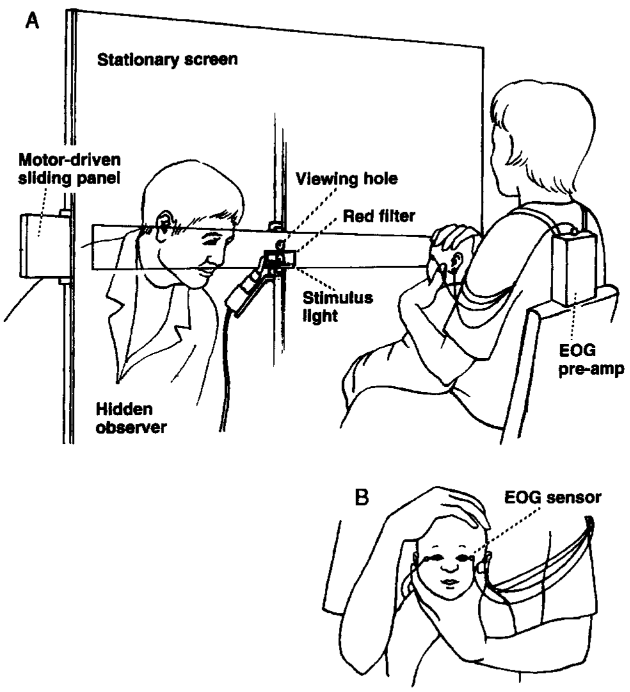

FIGURE 1. Experimental set-up. (A) An observer hidden by a screen activates a motor-driven panel containing a small target light when he sees through the viewing hole that the infant is attending to the target. The infant sits comfortably on the holder's lap and has her head restrained, as shown in (B). Placement of EOG electrodes is lateral to the eyes (B) with a ground electrode on the ear (A).

Following the calibration procedure, the control of target motion was switched to a servo system, which

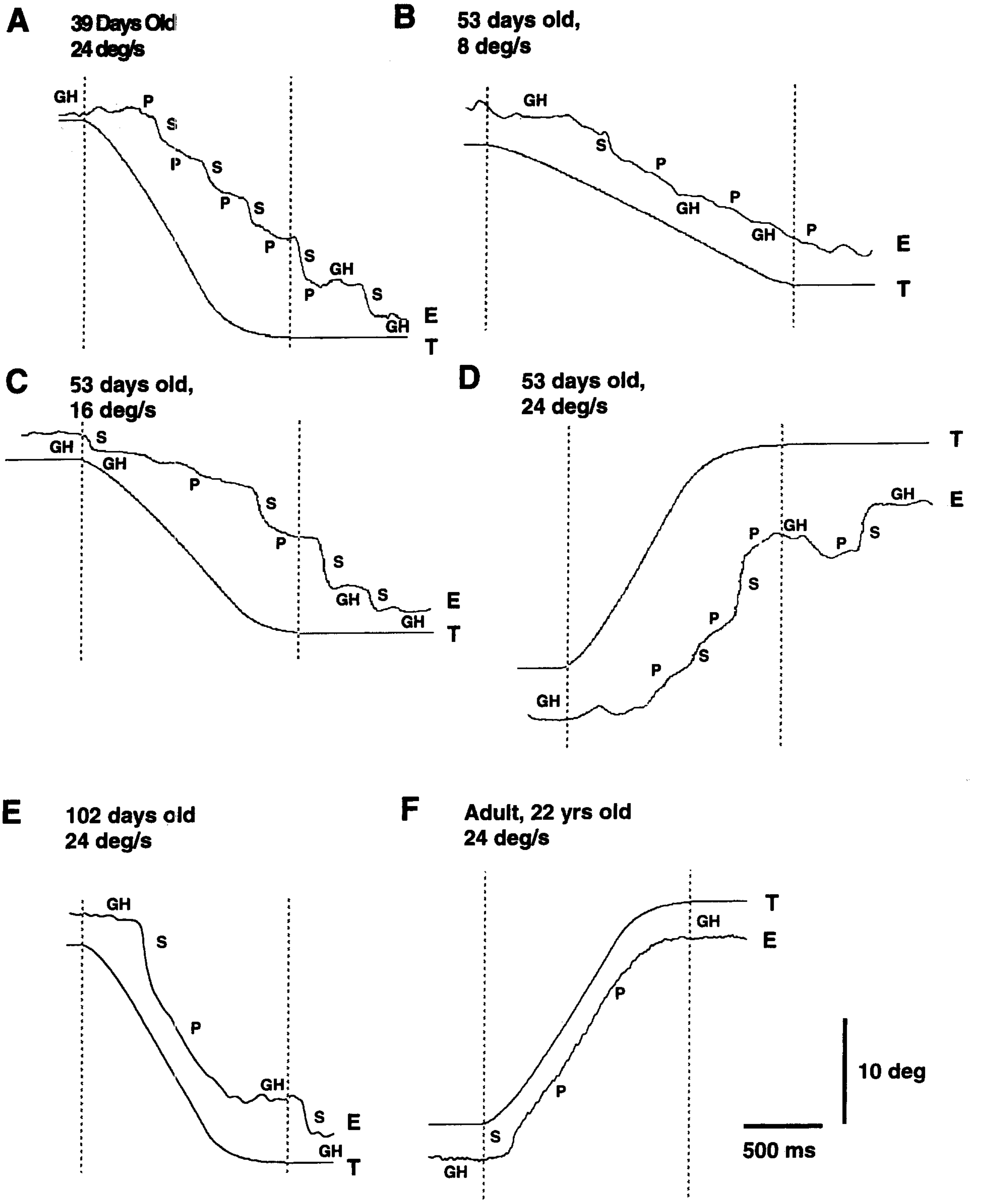

FIGURE 2. Representative eye-movement responses from a 39-day-old infant (A), a 53-day-old infant (B, C, D), a 102-day-old infant (E), and an adult (F) to hold–ramp–hold target movement at a variety of target velocities. In each panel, E and T indicate horizontal eye and target movement, respectively. Upward traces indicate rightward movement and downward traces indicate leftward movement. In all traces, S, P, and GH indicate saccades, smooth pursuit eye movements, and gaze holding, respectively. The shaded vertical lines indicate the start and stop of target movement. The vertical and horizontal calibration bars indicate 10 deg and 500 msec, respectively.

provided a hold–ramp–hold target motion. The hidden observer could control the amplitude ($\approx$20 deg; e.g., 10 deg left to 10 deg right of central position) and velocity of the ramp target motion (4–32 deg/sec), which was typically presented in blocks of 10–20 trials of alternating right- and leftward motion with constant motion parameters (e.g., ramp amplitude and velocity). Because of limitations in the servo system, there was an acceleration limit at the beginning and end of each ramp; however, the ramps of a given velocity and amplitude were essentially the same. While infants were encouraged to fixate the target light at each hold position by vocalizations, squeaks and rattles from the hidden observer, there was no moving auditory stimulus during the target motion. If at any time the infant subjects became fussy or hungry, they were returned to the parent who was present in the test room.

Analog voltages related to horizontal eye position, target position, on-target status, and voltage offsets of the EOG were filtered and passed through a PCM digitizer (Neurodata) which converted them to video signals for storage on VCR tape. For most smooth-pursuit analysis, the horizontal EOG (eye position) and the output of a potentiometer monitoring target position were filtered at 30 Hz with an 8-pole Bessel filter. For some trials, however, signals were filtered at 80 Hz to allow accurate measurement of saccadic amplitude and duration (Bahill *et al.*, 1981). The filtered signals were then digitized at 500 Hz or 1 kHz for later analysis on a Macintosh computer.

Data analysis was performed with an interactive program that displayed eye and target position. The color of the traces was controlled by the on-target and EOG-offset signals so the stimulus control of subject performance and any recording artifact could be assessed off line. The investigator analyzed files by manually moving a set of cursors through the data record and identifying epochs for analysis. Each epoch was categorized as either: (1) a smooth eye movement in the direction of target motion; (2) a saccade in the direction of target motion; (3) stable gaze holding; (4) a saccade in the direction opposite that of target motion; or (5) a smooth eye movement in the direction opposite that of target motion. A velocity of 40 deg/sec was the criterion used to identify saccadic eye movements. This value was obtained from the slowest spontaneous saccades in the dark. For each epoch, average velocities of eye and target, start and end positions, duration, and latency from eye to target start and end were determined. Data were then grouped according to age and ramp target velocity, and both parametric and non-parametric statistical analyses (non-paired T and Mann-Whitney tests) were performed to determine significant differences between groups.

RESULTS

General tracking characteristics and identification of smooth pursuit

All of the infant subjects, even the very youngest (3 weeks), moved their eyes toward the moving small light spot. In most subjects, the components of adult tracking were easy to recognize, even in the youngest infants [Fig. 2(A)]. As mentioned in the Methods, all movements with peak velocities >40 deg/sec were considered to be saccades ("S" in Fig. 2). Movements at lower velocities in the direction of target movement were taken as smooth pursuit ("P" in Fig. 2). If the eye stopped moving during a tracking segment, this epoch was not treated as a segment of zero-velocity smooth pursuit, but rather as a period of gaze holding ("GH" in Fig. 2). In the 39-day-old subject in Fig. 2(A), saccades and smooth-pursuit segments were easy to identify. In other subjects such as the 53-day-old infant in Fig. 2(B–D), tracking had occasional oscillatory segments, in which identification of separate saccades and smooth-pursuit segments was more difficult. Nevertheless, even for such infants, most trials showed clear segments of smooth pursuit.

The time course of the tracking responses and the relative contributions of smooth pursuit and saccades varied from trial to trial, from infant to infant, and from age to age. Nevertheless, most tracking eye movements had some common characteristics. A typical infant response [Fig. 2(A)] began with eye movement in the direction of target motion after a long delay of stable gaze holding. The first movement was often a saccade, but could also be smooth pursuit. Generally, after the first saccade there was a sustained period of smooth eye movement whose velocity was less than target velocity. Usually, this epoch was the longest smooth pursuit segment in the trial. The efficacy of the smooth-pursuit response, its *gain*, is measured as eye velocity/target velocity. For all infant smooth-pursuit segments identified in Fig. 2(A), the gain was <1.0. Because of the low smooth-pursuit gain, the eyes fell farther and farther behind the target and a succession of catch-up saccades and smooth eye movement or gaze holding epochs resulted. After the target had stopped, the eyes continued to move for a considerable time (the end-latency). The trial ended with a period of gaze holding (GH) with the target stationary.

By the age of 3 months, eye movement became increasingly dominated by smooth pursuit, and smooth pursuit had a higher gain. For example, in response to target ramps of comparable velocity, the older infant [Fig. 2(E)] clearly had longer, higher-gain epochs of smooth pursuit while the younger infant [Fig. 2(A)] relied more heavily on catch-up saccades. In all infants [e.g., Fig. 2(A, D, E)], smooth-pursuit gain was lower than that of typical adult smooth pursuit to the same stimulus [Fig. 2(F)]. With age, the latency from the onset of target motion to the onset of eye motion decreased, as did the persistence of smooth eye motion after the target stopped. By adulthood, eye movement latencies to the onset and end of target motion are shortest, smooth-pursuit gain is often near 1.0, and usually only one or no catch-up saccades are required [Fig. 2(F)].

Quantitative analysis of the tracking response

Infant tracking responses could be described by considering several different measures. First we assessed how well the stimulus engaged the infant by comparing the cumulative amplitude of all of the eye movements for a hold–ramp–hold trial with the amplitude of the target motion during that trial. Second, we assessed smooth-pursuit ability directly by measuring the velocities and

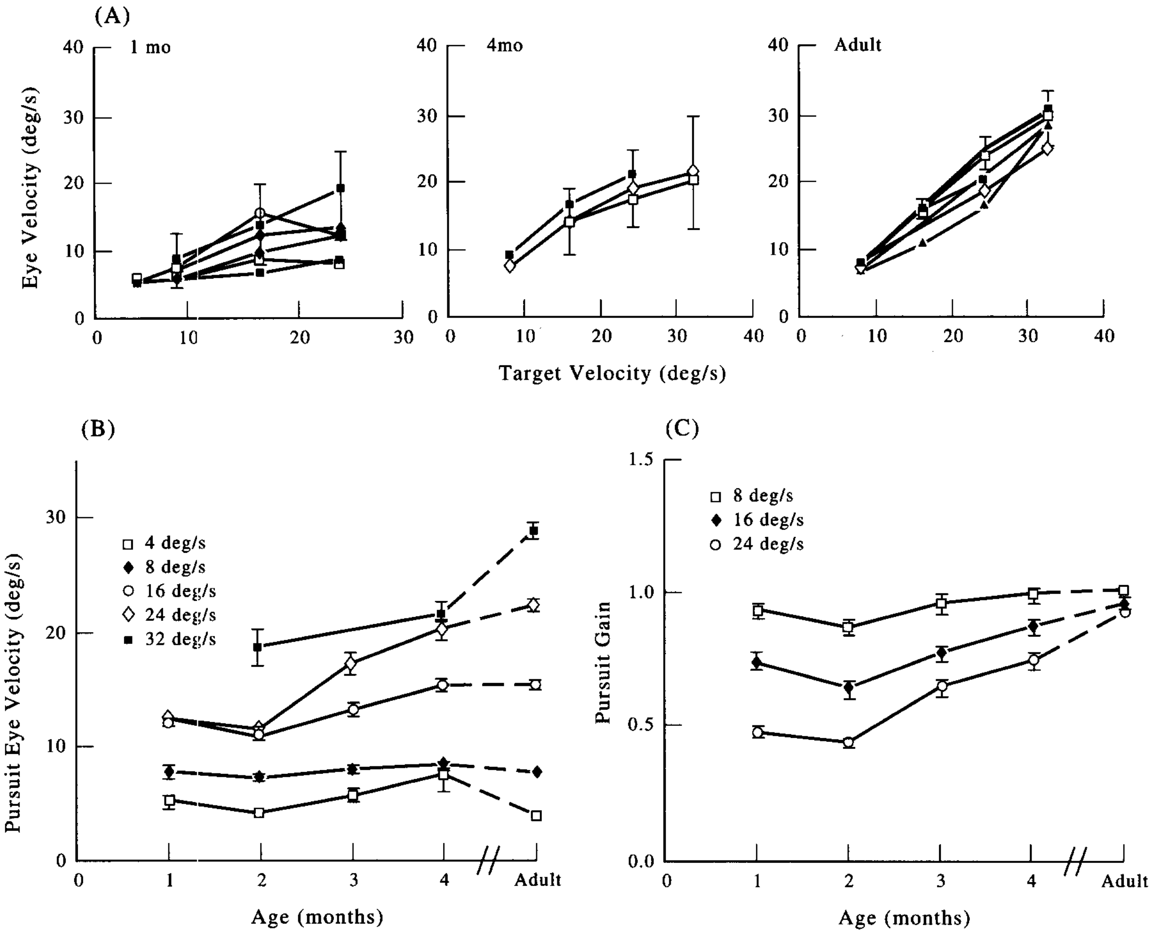

FIGURE 3. Characteristics of smooth-pursuit eye velocity and gain. (A) Smooth-pursuit eye velocity as a function of target velocity for several different subjects at three different ages. Even 1-month-old infants exhibited pursuit, which increased in magnitude to target velocities of ~ 16 deg/sec. Error bars indicate ± 1 SD for a representative subject. (B) Smooth-pursuit eye velocity as a function of age for different target velocities. (C) Smooth-pursuit gain as a function of age for three different target velocities. Error bars in (C) and (D) indicate ± 1 SEM.

gains of all the pursuit epochs in a tracking trial. Third, we determined the maximum capability of the smooth-pursuit system as the highest smooth eye velocity attained during each trial at each target velocity. Fourth, we ascertained the relative contributions of saccades and pursuit movements to the tracking response by determining the amount of time devoted to each epoch of pursuit, the percentage of trial duration occupied by smooth-pursuit epochs, the number of saccades seen during 20 sec of testing, and the average saccade amplitude. Finally, we assessed the speed of the transformation from the visual target movement to a tracking response as the latency of eye movement to the start and end of target motion. These latency measures also gave an indication of whether a subject anticipated or predicted the target motion.

Tracking performance

As a measure of overall performance on the pursuit task, we determined tracking gain as total eye movement during a hold–ramp–hold target movement divided by total target motion. Tracking gain ranged from 0.8 ± 0.2 for 2-month-old to 1.0 ± 0.1 for adult subjects at target velocities of 8 deg/sec. Lower target velocities (e.g., 2 deg/sec) did not elicit reliable responses, even in adults. At target velocities of 16 and 24 deg/sec, tracking gains consistently increased with increasing subject age. For example, at 24 deg/sec target velocities, tracking gains were 0.6 ± 0.2 for 1-month-old infants, 0.8 ± 0.3 for 3-month-old infants and 1.0 ± 0.1 for adults. At this target velocity, tracking gains were significantly different between all infant groups ($P < 0.0003$) except between 2- and 3-month-old infants. Adults differed significantly from all infants <4 months of age ($P < 0.0001$). Although we asked only ≥2-month-old infants to track targets moving at 32 deg/sec, we observed tracking gains above 0.9 for all subject groups, with significant differences between younger infants (aged 2 and 3 months) and adults ($P < 0.0089$). Clearly, infant and adult subjects tracked even our highest velocity target motion, indicating that our target motion parameters provided a compelling stimulus.

Smooth-pursuit operating range

As our first measure of smooth-pursuit capability, we determined the eye velocity for each smooth-pursuit

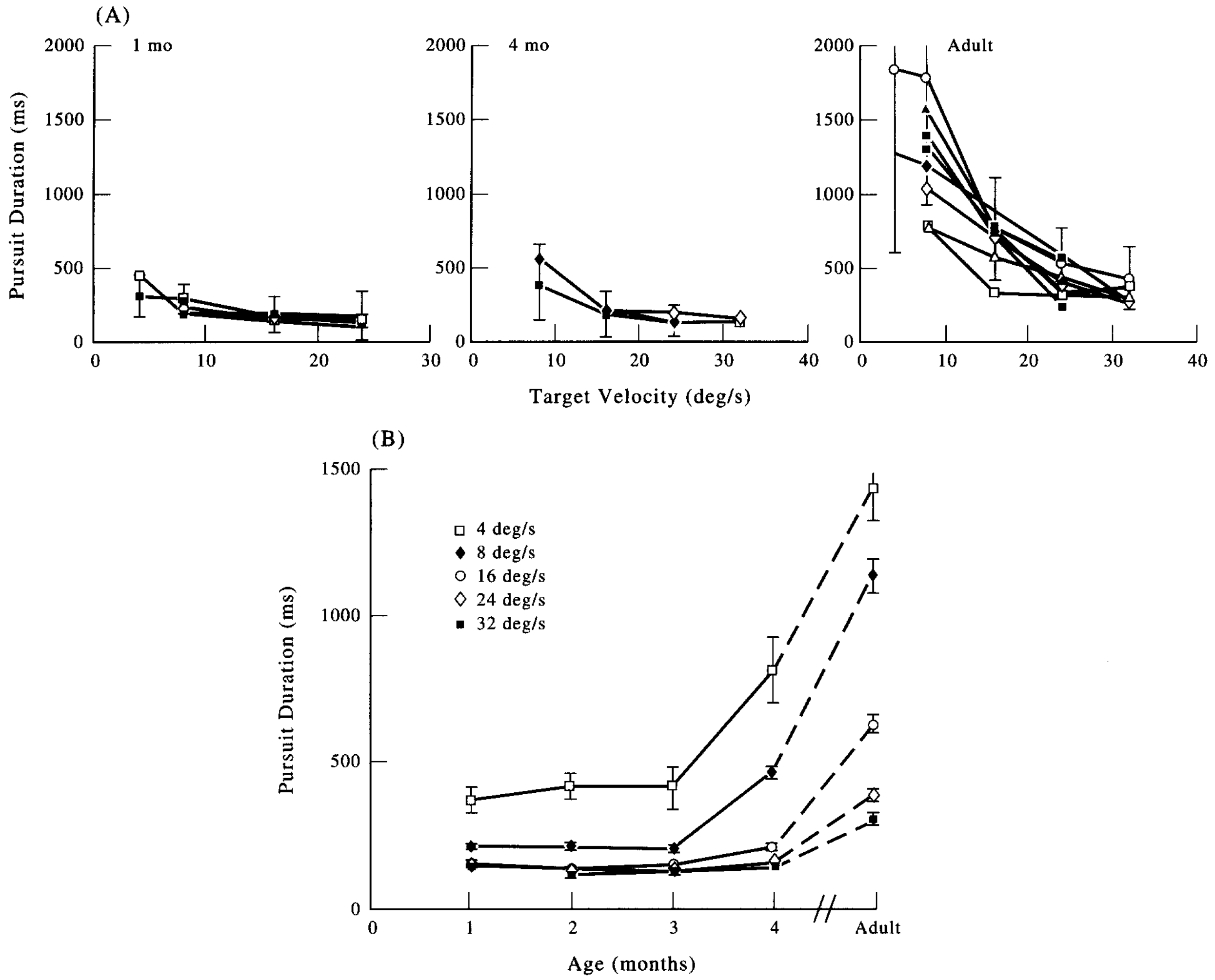

FIGURE 4. Durations of individual pursuit epochs during trials of ramp-and-hold target motion. (A) Duration of smooth pursuit vs target velocity for several subjects at three different ages. Error bars indicate ±1 SD for a representative subject. (B) Duration of smooth pursuit vs subject age at different target velocities. Error bars indicate ±1 SEM.

epoch and averaged the epoch eye velocities for each target velocity, infant and age. At all ages, average eye velocity increased with target velocity for each subject over at least part of the target velocity range tested [Fig. 3(A)]. For example, in 1-month-old infants, smooth-pursuit velocity increased with target velocity until target velocity reached ~16 deg/sec, where average eye velocity was 12.4 deg/sec. Target velocities of 24 deg/sec produced average smooth eye velocities of 12.2 deg/sec, suggesting that the average smooth-pursuit response saturated at ~12 deg/sec. About half of the 2-month-olds also exhibited a velocity saturation (mean ~15 deg/sec), whereas none of the 3- and 4-month-olds did [Fig. 3(A)]. Thus, older infants reached higher eye velocities for a particular target velocity. For example, targets moving at 24 deg/sec were tracked at an average speed of 11.3 deg/sec by 2-month-olds and 19.9 deg/sec by 4-month-olds. Indeed, at all target velocities >8 deg/sec, older infants attained higher smooth-pursuit velocities [Fig. 3(B)] and smooth pursuit was significantly related to age.

Average smooth-pursuit gain

For infants of ≤4 months of age, average pursuit gains decreased with target velocity. This can be seen most dramatically in the average for the 1-month-old infants [Fig. 3(C)]. At low target speeds (8 deg/sec), smooth-pursuit gain was remarkably constant across age groups, ranging from 0.88 at 2 months to 1.0 for adults. At higher target velocities (16 and 24 deg/sec), the gain increased for ages >2 months. For example, a target moving 24 deg/sec elicited average smooth-pursuit gains of 0.45 in 2-month-old infants and 0.77 in 4-month-olds. At this velocity, the smooth-pursuit gains at each age between 2 months and adulthood were significantly different ($P < 0.02$).

In summary, smooth-eye-movement gain increased with age for higher target velocities and decreased with target velocity at all ages.

Peak smooth-pursuit gain

Gain was higher during some smooth-pursuit epochs than during others. To obtain a measure of this "best"

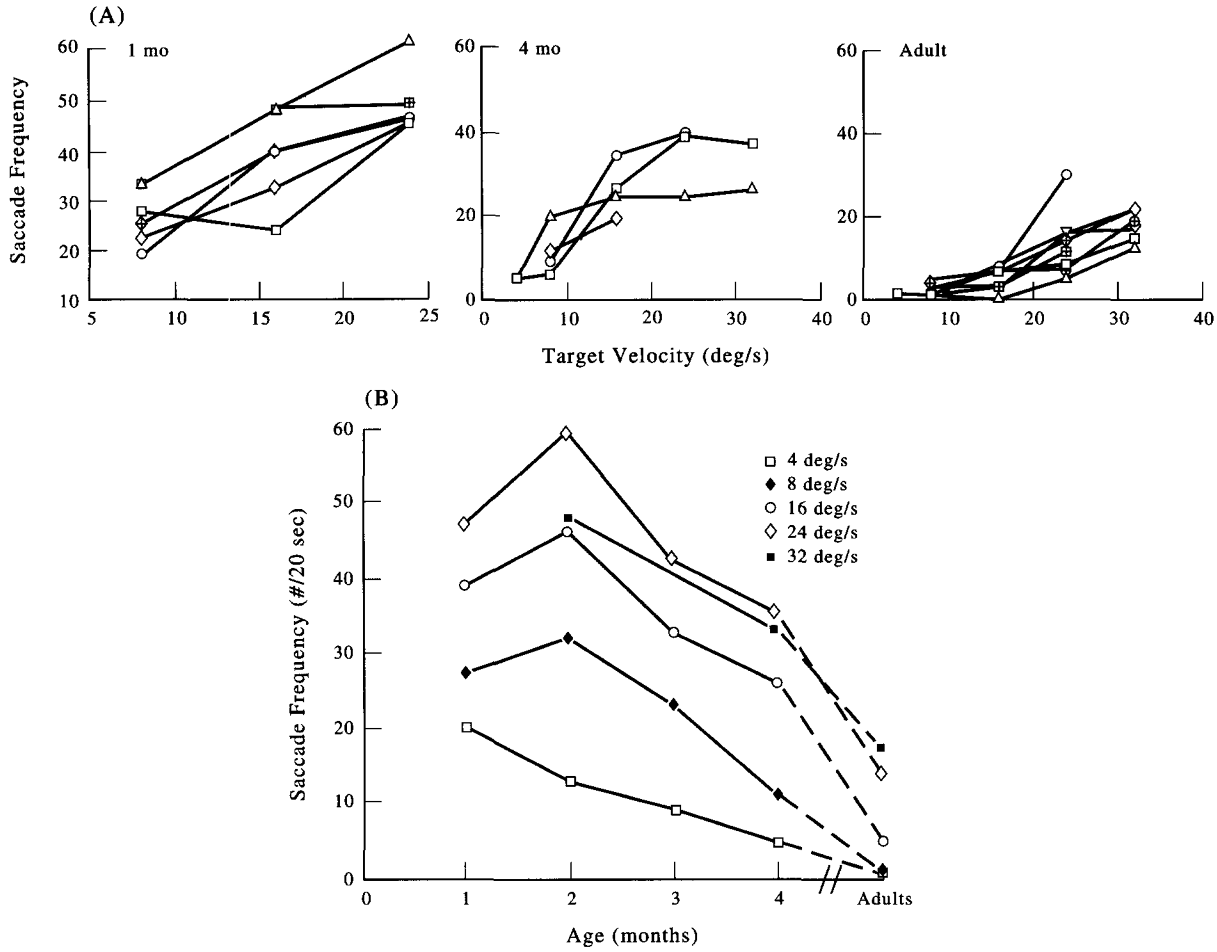

FIGURE 5. Frequency of catch-up saccades in the eye-movement response during tracking trials. (A) Number of saccades accumulated in 20 sec of tracking over several trials as a function of target velocity for several subjects at three different ages. (B) Number of saccades in 20 sec as a function of age for different target velocities.

smooth-eye-movement performance, we identified the epoch in each trial with the highest eye velocity (and hence gain) and averaged those peak gains for each set of trials at each target velocity in each subject. Peak eye-velocity gains were always greater than the average smooth-pursuit gain shown in Fig. 3(C). For example, target velocities of 24 deg/sec produced peak eye-velocity gains ranging from 0.6 in 1-month-olds to 0.9 in 4-month-olds. At lower target velocities the peak eye-velocity gains were even higher. For example, at target velocities of 16 deg/sec, the peak smooth-pursuit gain of 1-month-olds was 0.9. Thus, although the average smooth-pursuit gain of infants invariably was <1.0, individual epochs in many trials had eye velocities at or near target velocity.

Relative contributions of smooth pursuit and saccades to tracking

Smooth-pursuit duration. As target velocity increased, the amount of the tracking movement that constituted smooth pursuit decreased in both infants and adults. To quantify this observation, we added the durations of each epoch of smooth eye movement in individual trials at each subject age and target velocity. In infants <3 months of age, average pursuit duration within a trial varied little for velocities ≥16 deg/sec (Fig. 4B). For example, in 2-month-old infants, targets moving at 16, 24, and 32 deg/sec produced average smooth-pursuit epochs of 139, 136, and 120 msec, respectively. However, lower target velocities produced significantly longer pursuit epochs in this age group (405 msec for targets moving 4 deg/sec and 215 msec for targets moving 8 deg/sec).

There was little change in pursuit duration until 3 months of age. For example, when presented with targets moving 8 deg/sec, 1-, 2- and 3-month-old infants had average smooth-pursuit durations of 215–220 msec, whereas 4-month-old infants had average durations of 476 msec and adults of 1150 msec.

Of course, even relatively short epochs of pursuit could sum to produce a tracking response that was primarily composed of pursuit, although interrupted frequently by small saccades. To quantify the overall contribution of pursuit to the tracking response, we measured the percentage of the total trial duration over which the infant displayed pursuit. Infants spent less of the tracking response (≤63%) in smooth pursuit than did adults (≥82%), and 4-month-old infants spent more time, on

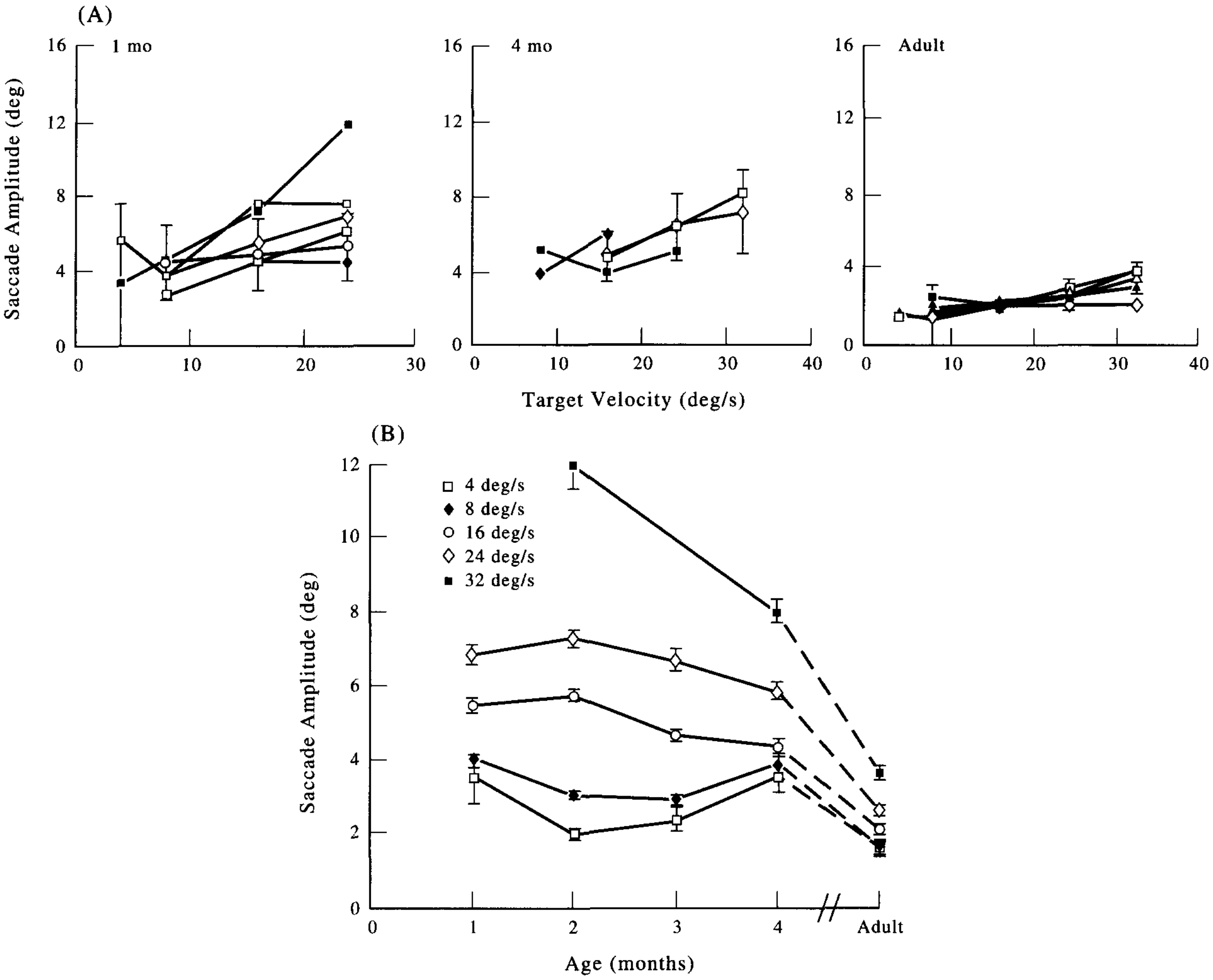

FIGURE 6. Amplitude of catch-up saccades in response to ramp-and-hold target movements. (A) Amplitude of individual saccades during a single tracking trial as a function of target velocity for several subjects at three different ages. Error bars indicate ±1 SD for a representative subject. (B) Saccade amplitude during a single tracking trial as a function of age for different target velocities. Error bars indicate ±1 SEM.

average, in smooth pursuit at each velocity than did 1-month-old infants (e.g., 63 and 61% versus 38 and 36% at 8 and 16 deg/sec). However, the percentage of time spent in smooth pursuit by 1-, 2- and 3-month-old infants was roughly constant. Similarly, there was no consistent change in the percentage of smooth pursuit with target velocity.

We also determined the percentage of trials in which only smooth pursuit occurred. For adult subjects, the percentage of trials with only smooth pursuit decreased as target velocity increased. For example, a target moving 32 deg/sec produced a pure smooth eye movement in 18% of the trials, but a target moving at 8 deg/sec produced pure smooth eye movement in 81% of the trials.

At all velocities, infants produced fewer trials of pure smooth pursuit than did adults. For all but one target velocity, infants aged 1–3 months produced pure pursuit trials $<15\%$ of the time. For trials with target velocities ≥ 4 deg/sec, pure pursuit trials never exceeded 3% of the total in these age groups. In 4-month-old infants, pure pursuit accounted for 28% of the trials at 4 deg/sec and 10% of trials at 8 deg/sec. At higher target velocities, there were no significant differences between 4-month-old and younger infants.

In summary, infants spent less time in each smooth-pursuit epoch and less time in smooth pursuit during the entire trial than did adult subjects. In the first 3 months of life, there is little change in the total duration of smooth pursuit, but in the fourth month, the duration increases toward that observed in adults.

Saccade contribution. As a measure of the saccadic contribution to infant tracking, we determined the average frequency of saccade occurrence over all trials and the saccade amplitude for different velocities, subjects and ages. Saccade frequency increased with target velocity to 24 deg/sec and decreased with subject age (Fig. 5). Saccade frequencies at each age and velocity were statistically different ($P < 0.05$). In all cases, saccade frequency was lower for adults than for infants, and lower for 3- and 4-month-old infants than for 1- and 2-month-olds [Fig. 5(B)]. For example, target motion of 24 deg/sec produced 2.4 saccades/sec in 1-month-olds, 1.8 saccades/sec in 4-month-olds, and only 0.7 saccades/

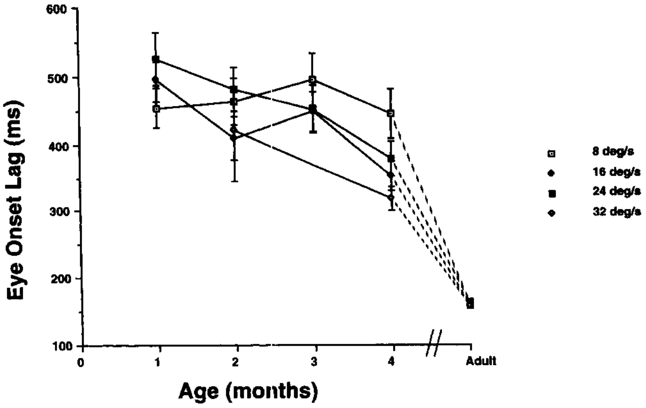

FIGURE 7. Latency from onset of smooth target motion to onset of eye movement. Latency as a function of age for different target velocities. Error bars indicate ± 1 SEM.

sec in adults. Therefore, infant tracking includes more saccades than does adult tracking.

Although saccades tend to decrease in number with age, infant tracking actually appears to use more saccades at some intermediate stages of its development. As we stated earlier, tracking gains increase with age. However, from 1 to 2 months, smooth-pursuit gain actually decreases slightly [Fig. 3(C)]. The improvement in tracking at 2 months is apparently the result of increased saccade frequency [Fig. 5(B)].

Because saccade frequency increases with target velocity, one might expect that saccade amplitude would increase as well, since saccade frequency would increase under conditions where the smooth eye velocity was trailing further and further behind target velocity. Indeed, saccade amplitude increased as target velocity increased in both adults and infants [Fig. 6(B)], though the increases were far greater in infants than in adults. For example, when target velocity increased from 8 to 32 deg/sec, saccade amplitude increased from 3 to 12 deg in 2-month-olds but only from 2 to 4 deg in adults.

Sensory-motor processing for tracking

Onset latency. We hoped to gain an insight into the maturity of the sensory-motor processing required for tracking by examining the timing of the tracking responses relative to target motion. Therefore, we measured the interval between the onset of target motion and the onset of the first eye movement in the direction of target motion, whether it was smooth pursuit or a saccade. Adults typically initiated tracking of targets moving at velocities >4 deg/sec at latencies of ~150 msec. On the other hand, 1-month-old infants initiated such movements at average latencies of 454–526 msec (Fig. 7). By 4 months of age, average latencies decreased to a range of 318–446 msec. For example, a target moving 24 deg/sec evoked eye movement in the direction of target motion at an average latency of 512 msec in 1-month-old infants and at 381 msec in 4-month-olds.

Pursuit end latency. Infants also took longer than adults to completely halt their eye movements once the target had stopped. We measured the latency from the end of target motion to the end of smooth eye movement. The pursuit end latency was relatively constant with target velocity for each infant age group. Also, the pursuit end latency decreased with age. For example, when a target that was moving 24 deg/sec stopped, smooth eye movement continued for 407 ± 33 msec in 1-month-old infants but for just 176 ± 33 msec in 3-month-olds. At this velocity, adult subjects always anticipated the end of target motion so their eyes stopped when the target did. This anticipation was observed only infrequently in infant subjects, for whom continued eye movement only served to reduce a retinal position error that had accumulated over the entire pursuit trial. While there was no consistent relation between target velocity and pursuit end latency, there was a consistent decrease in pursuit end latency with subject age for target velocities of >4 deg/sec.

DISCUSSION

Characteristics of early tracking responses

Our fundamental finding is that infants as young as 1 month of age are capable of following smoothly moving small targets with smooth eye movements. As has been reported by others, the smooth pursuit tends to occur in short segments, is inadequate for targets moving faster than 8 deg/sec and reaches velocities that are much lower than those of the target. Typical average smooth-pursuit gains for 1-month-old infants are 0.48 for targets moving 24 deg/sec. Because the smooth-pursuit gain is rather low, the oculomotor system attempts to keep pace with the target by using frequent catch-up saccadic eye movements. A combination of smooth pursuit and catch-up saccades also characterizes the tracking of smoothly moving targets by adults. Therefore, the eye-movement building blocks for the tracking response clearly are in place from the first month of life.

There are several limitations on the tracking response of infants. First, smooth-pursuit gain is low at velocities of >8 deg/sec. Not only is smooth-pursuit gain lower than that of adults, but the increase of smooth-pursuit velocity with target velocity saturates at low target velocities for the youngest infants. In the 1-month-old infants, this saturation occurred at 12 deg/sec. In contrast, the adults in our study were able to follow targets moving at 32 deg/sec and there are reports of adult smooth pursuit to 120 deg/sec (Lisberger *et al*., 1978). Second, the amount of smooth pursuit in most tracking responses of 1-month-olds is rather brief, constituting only about 40% of the tracking response, in contrast to 90% of the response of adults. Third, the tracking response is slow to be launched, with the earliest eye movement occurring as late as 500 msec after the target begins moving. In adults, a typical latency is ~150 msec. Clearly, improvement in tracking performance includes maturation of all these aspects of smooth-pursuit performance.

Do all aspects mature together?

The earliest response to smooth-pursuit insufficiency is two-fold. First, tracking gains increase due to increased saccade frequency. Second, the saturation of smooth-pursuit velocity for the highest target velocities is eliminated. The saturation limit of 12 deg/sec at 1 month of age is not present in older infants.

Between 1 and 2 months of age, most other smooth-pursuit parameters show little change. Pursuit velocity gains below the saturation limit remain relatively constant or decrease slightly [Fig. 3(C)], and the percentage of smooth pursuit in a tracking response does not change. The latency to the onset and offset of the target motion also is relatively unchanged. While the frequency of catch-up saccades increases for target velocities between 8 and 24 deg/sec [Fig. 5(B), see above], there is no increase in saccade amplitude.

Between the second and third months of life, pursuit velocity gains increase [Fig. 3(C)] and catch-up saccade frequency begins to decrease [Fig. 5(B)]. Saccade amplitudes decrease at the highest target velocities, but show no change at velocities of $\leq$24 deg/sec. The duration of smooth-pursuit epochs is unchanged, as is the total percentage of each trial comprising pursuit eye movement.

It is between the third and fourth months of life that the most dramatic changes in the evolving smooth-pursuit performance occur. During this period, infants continue to show increasing smooth-pursuit gain. The duration of smooth-pursuit epochs increases substantially and there is a significant increase in the percentage of the tracking response accomplished by smooth pursuit.

Despite these improvements, however, the tracking response at 4 months of age is still quite immature. Smooth-pursuit gains are high (>0.89) for lower target velocities, but fall to 62–77% of those of adults at velocities of $\geq$24 deg/sec. Smooth-pursuit durations are 45% shorter than those of adults. Catch-up saccades are 220% larger in size than those of adults. Tracking latencies are also more than twice as long as those of adults. Clearly, considerable maturation of the tracking response must continue to occur.

The timing of their smooth-pursuit response suggests that infants do not exhibit adult-like prediction of the termination of target motion. Infants typically continue their smooth-pursuit eye movements after the end of target motion, even for stimulus velocities that almost always produce early, anticipatory cessation of pursuit in adults. Perhaps infants do not exhibit an anticipatory slow-down of smooth pursuit because it would not be beneficial; if such a slow-down were to occur, it would simply serve to maintain the retinal position lag inherent in infant smooth pursuit (Fig. 2). On the other hand, a slow-down in adult smooth pursuit is beneficial; during adult smooth pursuit the eye exhibits little, if any, lag and the lag between eye and target would continue to be kept at a minimum if the eye could slow its motion in anticipation of the target stopping.

Comparison with other studies

The picture that emerges from this study is quite different from that presented in the last large-scale study of visual pursuit in infants. In that study, Shea & Aslin (1990) concluded that 7- to 11-week-old infants were capable of making smooth eye movements, but the youngest infants attempted to match only the direction and not the velocity of the smoothly moving targets. In contrast, our study shows that even very young infants (3–4 weeks of age) make low-gain smooth eye movements that increase in velocity as the target velocity increases. We conclude that infant pursuit behavior is limited in the range and gain of the eye velocities that are produced, but the behavior of infants is qualitatively adult-like.

We attribute the differences between our results and those of Shea & Aslin (1990) to methodological differences both in the elicitation of the eye movements and in the subsequent data analysis. In our study, we made the pursuit stimuli salient to the infants by providing auditory stimuli at the target location during the hold portion of the trials. Furthermore, we continually calibrated the eye-movement transducer during the trials by observing the infant's eyes at each hold position. Finally, we used simple ramp target motion, which reached a constant velocity only after a gradual acceleration phase. This stimulus may be far easier for infants to track than a target that first jumps in one direction and then commences moving at a constant velocity in the other, i.e., a step-ramp stimulus (Shea & Aslin, 1990).

In our analysis, gaze holding was not considered to be pursuit movement with zero velocity. Shea and Aslin consider all non-saccadic eye movements during target motion to be smooth pursuit. As we have shown, there are long intervals after the onset of target motion when the infant has not yet moved its eyes. We scored these latent periods, as well as other zero velocity segments during the tracking response, as gaze holding and not pursuit.

Earlier studies of infant pursuit have not produced consistent results. Aslin (1981), Dayton and colleagues (Dayton & Jones, 1964; Dayton *et al.*, 1964), and McGinnis (1930) reported virtually no smooth pursuit during tracking of smoothly moving targets in infants <2 months of age. Dayton & Jones (1964) specifically found that a ramp stimulus moving at 16 deg/sec produced no smooth eye movement in infants <8 weeks of age. This is in sharp contrast to our observations. Kremenitzer *et al.* (1979), on the other hand, did observe segments of smooth pursuit in newborn infants who were tracking a large stimulus moving 12 deg/sec, and Roucoux *et al.* (1983) reported smooth eye movement in 1-month-old infants that were tracking a 10-deg diameter Mickey Mouse head. Investigators who observed no smooth pursuit typically used higher velocities (10–40 deg/sec), while those who did observe pursuit used lower velocity target motion. As shown in Fig. 2, we found that 4-week-olds can use pursuit to track targets moving at $\leq$24 deg/sec. Thus, our data seem to confirm the results of

Roucoux *et al.* (1983) and Kremenitzer *et al.* (1979), extending those results to small, presumably pure pursuit, stimuli.

Implications for visual development

Our data show that smooth pursuit in 4- to 8-week-old infants is nicely related to target velocity. This is surprising, given the current belief that visual motion processing of small stimuli is largely absent in such infants. Newborn infants clearly generate slow optokinetic (optokinetic nystagmus, OKN) eye movements in response to large, full-field stimuli (Dayton *et al.*, 1964; Kremenitzer *et al.*, 1979; Atkinson & Braddick, 1981; Schor, 1993; Schor *et al.*, 1983), suggesting that they can process large-field moving stimuli. However, their capacity to do so is generally thought to be mediated subcortically because infants <3 months of age show directional asymmetries in monocular OKN (nasal-ward stimuli work better than temporal-ward stimuli; Atkinson, 1979; Atkinson & Braddick, 1981; Schor *et al.*, 1983; Phillips *et al.*, 1995), which, in the cat, can be attributed to asymmetric directional sensitivity of pretectal neurons. A symmetric OKN in the cat requires descending input from the cortex (Distler & Hoffmann, 1992), as does smooth pursuit in primates (Dursteler & Wurtz, 1988). Our smooth-pursuit data suggest that cortical processing of motion is functional in infants as young as 1 month of age.

Based on smooth pursuit of small targets, we suggest that most psychophysical studies underestimate the capacity of young infants to utilize image motion. Infants <2 months old show poor sensitivity to low-velocity image motion (Kaufmann *et al.*, 1985; Aslin *et al.*, 1988; Dannemiller & Friedland, 1989, 1991; Wattam-Bell, 1990). However, many of these studies based their conclusions on the detection of differential motion. For example, Wattam-Bell (1990) demonstrated that 8- to 9-week-old (~2 month-old) infants could detect differential motion of 12 deg/sec. In contrast, our 2-month-old subjects exhibited an increased pursuit velocity as target velocity was increased from 4 to 32 deg/sec. Since the ability to alter smooth-pursuit velocity must be based on an assessment of target motion, our eye movement data indicate that motion processing is more advanced than has been demonstrated by psychophysical studies.

A more immature motion processing capability also is indicated in studies based on visual evoked potentials (VEP; Wattam-Bell, 1988, 1991; Norcia *et al.*, 1991). In these studies, some infants display VEP patterns consistent with a detection of low-velocity (5 deg/sec) stimuli at ~2.5 months of age and higher velocity (20 deg/sec) stimuli at >3 months of age (Wattam-Bell, 1991). Thus, VEP indicants of the motion processing of 5–20 deg/sec stimuli appear at much later ages than does smooth-pursuit ability to track targets moving at 24 deg/sec (Fig. 2).

Our study suggests that visual motion detection and velocity estimation capabilities in very young infants may be far more developed than was believed heretofore. From our results, we suggest, first, the use of simple small stimuli like ours for examining visual motion detection in infants because such stimuli clearly elicit eye movements based on the processing of visual motion. Second, the effect of varying target motion conditions on the pursuit response should be examined. For example, does the presence of a projected visual background affect pursuit performance in infants more dramatically than it does in adults (Collewijn & Tamminga, 1983; Tamminga & Collewijn, 1981)? Will monocular presentation of pursuit stimuli produce directional asymmetries in the pursuit response indicative of immature cortical processing? Finally, infant smooth pursuit should be examined in the more natural condition in which targets are tracked with both eye and head movements (see von Hofsten & Rosander, 1996). Answers to these questions may help to further reconcile the variety of often conflicting observations about infant eye-movements performance.

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