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Development of Smooth Pursuit Tracking in Young Infants

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Eye and head movements were measured in a group of infants at 2, 3, and 5 months of age as they were attentively tracking an object moving at 0.2 or 0.4 Hz in sinus or triangular mode. Smooth pursuit gain increased with age, especially until 3 months. At 2–3 months, the lag of the smooth pursuit was small for the sinusoidal motion but large for the triangular one. At 5 months, smooth pursuit was leading the sinusoidal motion and the lag for the triangular one was small. Head tracking increased substantially with age and its lag was always large. © 1997 Elsevier Science Ltd.

Eye movements   Infants   Smooth pursuit   Saccades   Head movements

INTRODUCTION

Smooth pursuit is an important part of the visual attention mechanism, and its function is to stabilise gaze on a moving target. This is accomplished by moving gaze at ideally the same angular speed as the image of the visual target. In general, both eye and head movements are included in smooth pursuit. It includes a prediction process to overcome the processing lags and the mechanical lags of the system (Stark, 1968; Guitton *et al.*, 1990). Therefore, regular, periodic motions are better pursued than randomly determined ones (Bahill & McDonald, 1983; Buizza & Schmid, 1986; Collewijn & Tamminga, 1984). This advanced and complex oculomotor behaviour is first observed in human infants during their first months of life but little is known about its development. The purpose of the present study was to investigate this problem further.

Some tracking ability is present in the neonate but for targets of limited size it seems to be primarily saccadic. Dayton & Jones (1964) found that neonates pursued a wide angle visual display with smooth eye movements but the pursuit became rather jerky for a target of 16 deg moving at 15 deg/sec. Other studies have supported these findings. Kremenitzer *et al.* (1979) found that neonates would smoothly track a 12 deg black circle at 9–30 deg/sec, however, with low gain and only approximately 15% of the time. Roucoux *et al.* (1983) using a target covering 2–10 deg of visual angle found evidence of smooth pursuit in 1-month-old infants, but only at velocities of about 10 deg/sec or less and with low gain (<0.5). Bloch & Carchon (1992) used a red transparent ball covering 4 deg of visual angle and moving at a speed of 9 deg/sec. They found only saccadic tracking in neonates. Similar findings were reported by Aslin (1981) who used a black bar 2 deg wide and 8 deg high moving sinusoidally (lowest velocity 10 deg/sec) in a horizontal path. He found only saccadic following of the target up to 6 weeks of age after which smooth pursuit started to be observed. Phillips *et al.* (1994) demonstrated smooth pursuit for a small target (1.7 deg) moving slowly, 1 deg/sec in a 4 week-old infant. Finally, Shea & Aslin (1990) found some smooth pursuit for a 2 deg step-ramp target in 7 to 11-week-olds. Gain was found to be 0.25 at 6 deg/sec and 0.11 at 12 deg/sec.

The earliest expressions of smooth pursuit do not seem to predict the target motion very well. von Hofsten & Rosander (1996) found that the tracking by 1-month-old infants of a wide angle, sinusoidally moving stimulus was associated with a substantial lag of approximately 180 msec which was found to get systematically smaller with age. At least some of the 2- and 3-month-olds were able to extrapolate the motion of the visual stimulus, which was a sinusoidally moving, wide angle, vertically striped pattern with a centrally placed 7 deg fixation target. For limited size, sinusoidally moving targets, Aslin (1981) observed that the smooth pursuits obtained for 10-week-old infants lagged the target but not always the ones for 12-week-olds. At that age, he observed that the eyes often remained on-target or could even be slightly ahead of it.

Earlier research has indicated that the head is recruited in the earliest expressions of smooth pursuit but only to a minor degree. von Hofsten & Rosander (1996) showed that head movements contributed to the tracking behaviour of 1-month-old infants and that this contribu-

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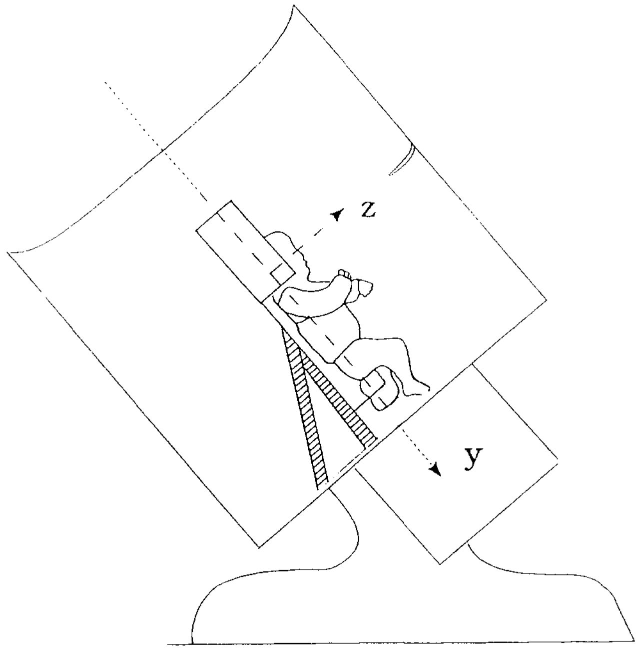

FIGURE 1. Lateral view of the positioned subject. The cylinder was 100 cm high and had a diameter of 100 cm. Distance eye–cylinder was approximately 40 cm. During the experiment the chair and cylinder were inclined at 40 deg to the vertical. The x-axis is perpendicular to the yz-plane.

tion increased from 1 to 3 months of age. Other observations indicate that the importance of head movements increases significantly over the next few months of life. Daniel & Lee (1990) studied tracking in 11–28-week-old infants and found that some of their oldest subjects used almost entirely head movements.

As discussed above, young infants seem to use catch-up saccades to correct for the imperfections of their smooth pursuit. However, little is known about the efficiency of these catch-up saccades. A number of studies have been performed on saccadic movements in young infants involved in redirecting gaze (Salapatek *et al.*, 1980) but all of them have used stationary targets. These saccades are of rather fixed size in young infants. Can catch-up saccades be characterised in a similar way, or do they scale to the velocity of the motion tracked?

In the study described here, a group of infants was studied at 2, 3 and 5 months of age. The starting age was decided from earlier reports cited above indicating that the development of smooth pursuit was definitely progressing at 2 months. The infants were presented with sinusoidal and triangular horizontal motion of different amplitudes and frequencies. The timing relationships between eye and target for these two motion functions reveal properties of the prediction process. Local extrapolations only function for continuously changing motion like the sinusoidal one. Triangular motion can only be predicted through a process that utilises the periodicity of the motion or a rule that informs the infant where or when the motion is going to turn ahead of time. The frequency of the target motion was either 0.2 or 0.4 Hz. Within this range the adult smooth pursuit system functions optimally but at frequencies above 0.4 Hz it starts to deteriorate (Barnes, 1993).

The following basic questions were asked: How does the tracking of a moving target improve over the studied age range and what is the relative contribution of head movements, smooth pursuit eye movements, and saccades. How are head movements and smooth pursuit eye movements timed relative to target motion? Do infants show signs of predictive tracking and at what age does it appear?

METHODS

Subjects

Eleven healthy and full-born infants were included in the study. When they were first seen, their age varied between 9 and 10 weeks (mean age was 2 months and 8 days). In the text they are referred to as 2-month-olds. Ten of them were then seen when aged between 14 and 16 weeks (on average 3 months and 9 days). In the text they are referred to as 3-month-olds. Finally, all 11 subjects were seen when they were between 4 and 5 months of age. Nine of them were between 20 and 21 weeks, one was 22 weeks and one was only 18 weeks. The average age of the whole group on this occasion was 4 months and 23 days. In the text they are referred to as 5-month-olds. Another four infants were seen at 2 months of age but two of those were not able to come for another visit and two were excluded because of fussing. Before each experimental session the parents of the infant signed a written consent. At the start of each experiment, the infant had been fed recently and was assured to be in an alert state.

Apparatus

The experiment was performed in an apparatus described earlier by von Hofsten & Rosander (1996). It consisted of an infant chair surrounded by a cylinder constituting a visual surrounding on which a visual target could be moved (see Fig. 1). The head of the infant was lightly supported with pads so that it could rotate without falling aside.

The inside of the cylinder was homogeneously white, except for a narrow horizontal slit right in front of the infant's face. The slit was 60 cm long and 1.5 cm wide (2.1 deg of visual angle) and had a movable object placed in it. This was a circular yellow happy face, 7 cm in diameter corresponding to a visual angle of approximately 10 deg, with a black contour around it. In the middle of the schematic face, a mini video camera (Panasonic WV-KS 152) was placed. Its black front had a diameter of 15 mm or 2.2 deg of visual angle. During the experiments, this video camera monitored the face of the infant. As it moved with the object and was always directed at the face of the infant, it was possible to determine whether the infant was paying sufficient attention to the object. The motion of the object was driven by a motor connected to a sweep function

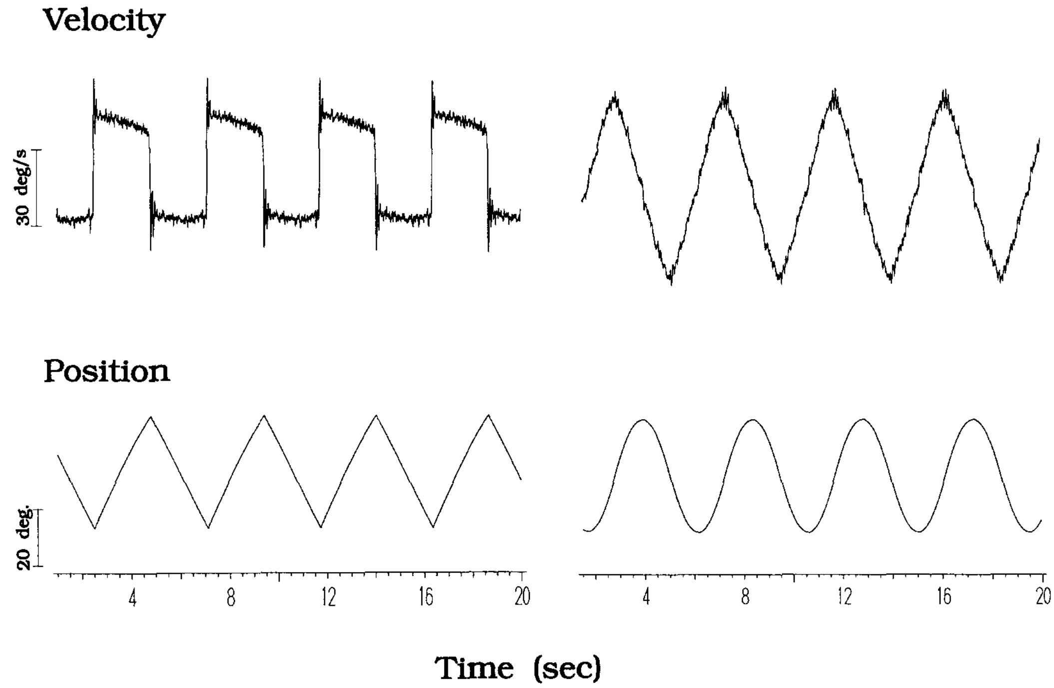

FIGURE 2. Position and velocity profiles of the sinusoidal and triangular motions used in the study.

generator. Before each trial the amplitude, frequency and type of motion of the object was set manually.

Stimuli

The target moved back and forth in front of the infant either according to a sinusoidal or a triangular motion function. The frequency of the motion was either 0.2 or 0.4 Hz and the amplitude either 10 or 20 deg arc corresponding to 12.5 or 25 deg of visual angle. All motions were produced by a mechanical device and therefore the sinusoidal and the triangular motions were not perfectly in accordance with the intended motion function. This can be seen in Fig. 2. The sinusoidal velocity change was slightly distorted toward more pronounced maxima and on the right side—(upper in Fig. 2) the velocity of the triangular motion decreased slightly towards the end of the motion path (about 10%). For sinusoidal motion, the maximum speed of the target in visual angle was 16 deg/sec in the 0.2 Hz–10 deg conditions, 33 deg/sec in the 0.2 Hz–20 deg and the 0.4 Hz–10 deg condition, and 65 deg/sec in the 0.4 Hz–20 deg condition. For triangular motion the velocity of the target was approximately constant during the full extent of each motion (however, see Fig. 2). The velocity corresponded to 10 deg/sec in the 0.2 Hz–10 deg condition, 20 deg/sec in the 0.2 Hz–20 deg and the 0.4 Hz–10 deg conditions, and 40 deg/sec in the 0.4 Hz–20 deg condition.

Measurements

Head and target motions. An opto-electronic device, Selspot (Selcom AB, Partille, Sweden) was used to monitor the movements of the head of the subject and the target. The signal-emitting part of the system consisted of infrared light emitting diodes (LED) of 4 mm in diameter. For details see von Hofsten & Rosander (1996). Two LEDs were used to record head position of the infant, and a third LED was placed on the target to record its motion.

Electro-oculographic recording and calibration. The EOG amplifying system was designed in collaboration with G. Westling (Dept of Physiology, Umeå University). For details see von Hofsten & Rosander (1996). The electrodes were of miniature type (Beckman) and were attached to the outer canthi. The ground electrode, a standard EEG child electrode, was placed on the ear lobe.

The EOG signal was calibrated in the same way as described earlier (von Hofsten & Rosander, 1996). The experimenter started at the centre (0 deg) and then moved the "happy face" (the target) to an intermediate position at the side (16 deg of visual angle) and to a more extreme position (24 deg of visual angle). Then it was again moved to the intermediate position, the centre, the intermediate position on the other side, and the extreme position on that side, etc. After the target had stopped at each new location, it was shaken a little to attract the infant's gaze. Each stop lasted 1–2 sec and if there was any doubt that the infant's fixation was on the target, it was shaken a little further. During the 20 sec period of data collection the experimenter covered about 1.5 cycles of motion in this way (right–left–right–left) corresponding to 12 fixation stops. During the calibration procedure, data were collected from the EOG and the LEDs on the target and the head simultaneously.

Experimental procedure

The infant was placed in the seat with the EOG electrodes and the two LEDs properly attached. After placing the cylinder in front of the infant, the first calibration trial was run followed by one trial in each of the eight experimental conditions. The order between the trials was randomised. Data were collected for 20 sec at 200 Hz. Between each trial, the base level of the EOG signal was adjusted when the infant looked straight ahead. The total duration of an experimental session was about 10 min.

Accuracy of experimental data

The position accuracy of each SELSPOT measurement was approximately ± 0.2 deg of head angle and the velocity data of approximately ± 0.8 deg/sec. It was not possible to determine an absolute accuracy of the EOG but estimates indicated an accuracy of around ± 0.4 deg for position and ± 1.5 deg/sec for velocity.

EOG calibration. Multiple calibration values were calculated from the different parts of the calibration trial. Head movement amplitude was first subtracted from target motion amplitude. The remaining change was the value against which the EOG change was calibrated. A correct value presupposed the subject to fixate the same part of the happy face before and after the position change. It was not possible to determine whether this was valid for a single interval. However, multiple such values were calculated for the multiple intervals, over shorter as well as longer intervals. If the infant changed fixation from the centre of the face to the periphery or from one periphery to the other, the calibration value for that specific short interval would become grossly different from the ones where approximately the same area was fixated (50% or more). The final calibration was based on the median of calculated values which implies that such outliers were automatically discounted. Most of the calculated values clustered rather close together. The average quartile deviation in per cent of the median value was 4.6, 3.5 and 3.8% for the 2-, 3- and 5-month-old infants, respectively. This corresponds rather well to a spread of fixations within the central area of the "happy face" which included the eyes, nose (the video camera), and the smiling mouth (5 deg of visual angle). Systematic overestimation or underestimation of the final calibration value would only occur if the infant preferred to fixate different parts of the "happy face" at different target positions and that those preferences shifted systematically and evenly with target position. It is important to note that the infants not only tracked the target from one position to the next. Shaking the target actually made them refixate it.

One indication that the median reflected the true gain fairly well was the fact that the added gain of eye and head (i.e., gaze) showed little variance even when head gain varied much between trials. If eye gain was overestimated, a greater proportion of the tracking accounted for by eye movements would produce a greater overestimation of gaze gain. The opposite is also valid. Such covariation between eye gain and head gain was not observed.

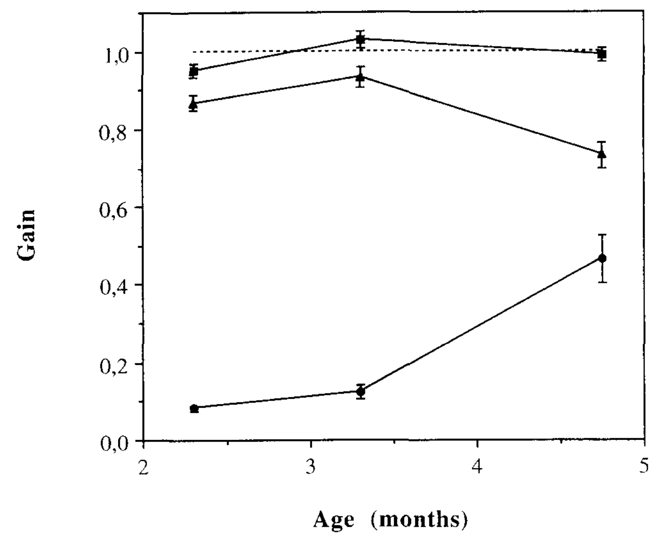

FIGURE 3. Mean and SEM calculated over all experimental conditions of position gain of gaze (squares), eye (triangles), and head (circles) movements for each age level.

Data analysis

The videotapes were examined to decide whether a trial should be included or disregarded. Parts of trials where the subject fussed or looked away from the target were disregarded. If the duration of any tracking period during a trial was less than 1.5 cycles (corresponding to 7.5 sec at 0.2 Hz and 3.75 sec for the 0.4 Hz motions), then the whole trial was disregarded. Only experimental sessions with more than four acceptable trials were included in the analysis. For this reason the records of five of the infants were excluded at 5 months of age.

Of the experimental sessions included, five individual trials were excluded at 2 months of age, two at 3 months of age, and four at 5 months of age. The records of the target motion were lost for one infant at 2 months of age and, therefore, only gain analysis could be performed in that case. Data analysis was performed using a program specially designed for time series, FYSTAT (Lars Bäckström, Dept of Physiology, Umeå University). For details see von Hofsten & Rosander (1996).

Saccades and smooth pursuit. The gaze was estimated as the sum of eye and head positions. Angular velocities were estimated as the difference between consecutive coordinates. Each velocity value was the mean difference between four time samples corresponding to a 50 Hz filter. The velocities of the eyes, head, and target were routinely calculated in this way. Saccades were defined as periods of the eye velocity record higher than 50 deg/sec of the tracking velocity amplitude. This criterion was used because we wanted to cut the saccades as close to their base as possible. We found that a still lower criterion started to cut the peaks of the smooth eye movements. Average amplitude and number of saccadic periods were calculated. To calculate the smooth pursuit component, the saccades defined in this way were eliminated from the composite, raw eye movement record. The periods cut out were replaced with interpolated data.

TABLE 1. *F* ratios for the main effects and the simple interactions between experimental variables

	Age	Target frequency (*f*)	Target amplitude (*a*)	Type of motion (*m*)	*f*× *a*	*f*×*m*	*a*×*m*
Gain of gaze	n.s.	5.26 (1,23)[a]	10.51 (1,23)[b]	n.s.	9.17 (1,23)[b]	6.65 (1,23)[a]	n.s.
Gain of eye	4.72 (2,23)[a]	11.29 (1,23)[b]	13.79 (1,23)[c]	11.92 (1,23)[b]	n.s	n.s	n.s
Gain of head	9.65 (2,23)[c]	6.21 (1,23)[a]	4.93 (1,23)[a]	n.s	n.s	n.s.	n.s.
Proportion smooth pursuit	7.01 (2,23)[b]	79.7 (1,23)[c]	44.9 (1,23)[c]	n.s.	7.42 (1,23)[a]	13.39 (1,23)[b]	n.s.
Amplitude of saccades	ns[a]	69.9 (1,23)[c]	140.5 (1,23)[c]	n.s.	34.6 (1,23)[c]	n.s.	n.s.
Frequency of saccades	n.s.	139.6 (1,23)[c]	80.45 (1,23)[c]	6.98 (1,23)[a]	n.s.	n.s.	n.s.
Timing of smooth pursuit	11.48 (2,22)[c]	n.s.	9.90 (1,22)[b]	83.6 (1,23)[c]	n.s.	4.63 (1,23)[a]	5.03 (1,23)[a]

Degrees of freedom are shown within parentheses. n.s., not significant.

[a]$P<0.05$.

[b]$P<0.01$.

[c]$P<0.001$.

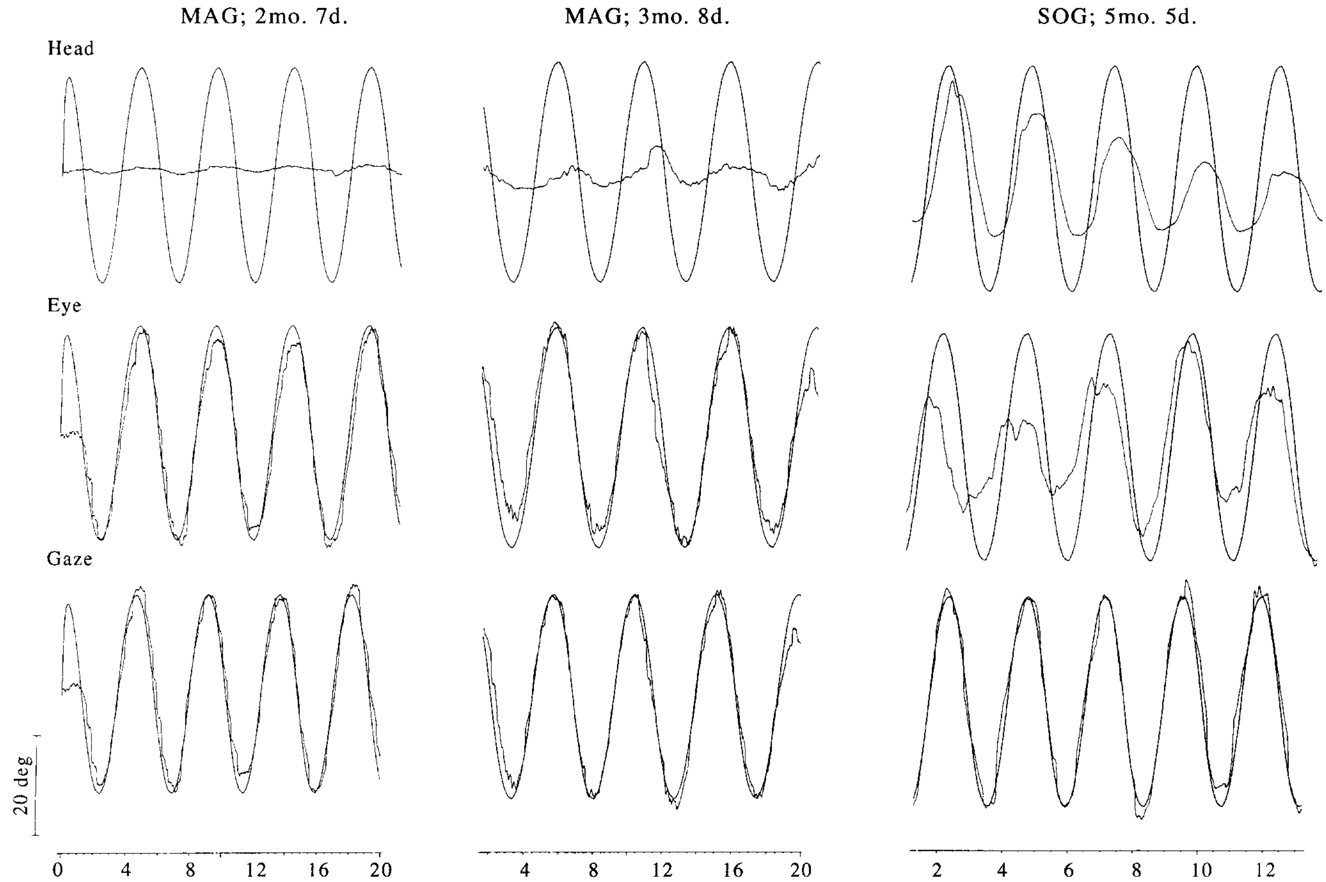

FIGURE 4. Examples of typical pursuit tracking of the sinusoidal motion. Note the increased involvement of the head with age. At 2- and 3 months of age MAG is tracking the high amplitude 0.2 Hz target and at 5 months of age SOG is tracking the high amplitude 0.4 Hz target. The position gains of the head, eye, and gaze for MAG at 2 months were 0.02, 0.92, and 0.94, respectively. Corresponding values for MAG at 3 months were 0.10, 0.89, and 0.96, and for SOG at 5 months 0.45, 0.66, 1.00.

Gain. The gain of eye, head, and gaze angular positions or velocities was estimated as the ratio of the Fourier analysed amplitudes of the signal and the target at 0.2 or 0.4 Hz.

Proportion of smooth pursuit. Proportion of smooth pursuit was calculated as the ratios of gains with and without saccades. The estimates obtained are rather insensitive to possible calibration errors of the EOG. Saccades were on the whole much larger than the cut-off and even a 10% shift made very little difference for the detection of saccades. Furthermore, a saccade detected by a 50 deg/sec cut-off and not by a 55 deg/sec cut-off (10% difference) corresponded to a very small position change. Such a tip of a small saccade would only have a duration of 25 msec or less and the cut-off part would then only cover about 0.1 deg of eye movement.

Time relations. Time coincidence relationships were evaluated with cross-correlation analysis. The lag or lead of the head was related to the target. The task of the eyes is to track the target relative to the head, which means that

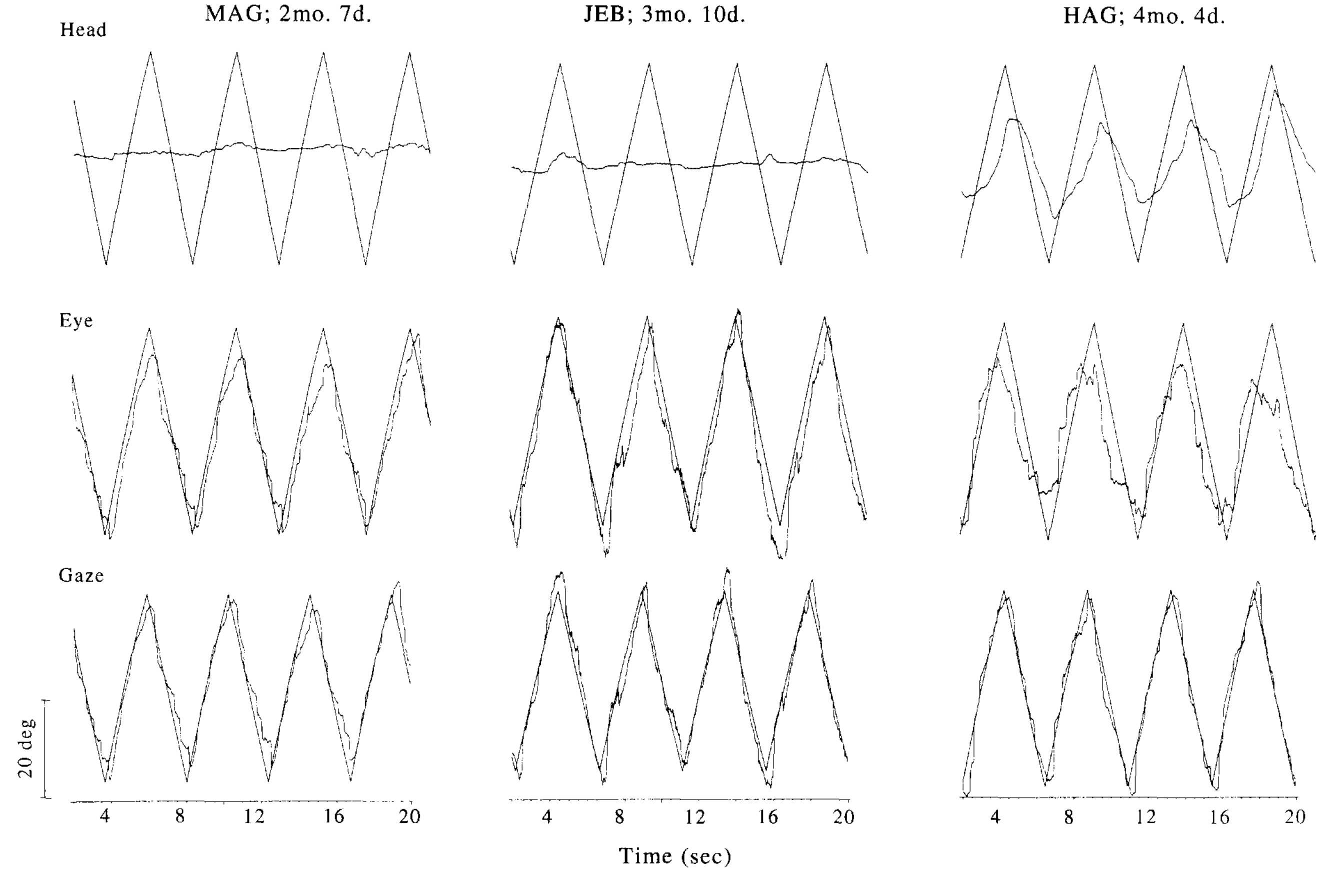

FIGURE 5. Examples of typical pursuit tracking of the triangular motion at 0.2 Hz, high amplitude. Note the increased involvement of the head with age. For MAG at 2 months the position gains of the head, eye, and gaze were 0.03, 0.85, and 0.88, respectively. Corresponding values for JEB at 3 months were 0.11, 0.90, and 0.99, and for HAG at 4 months 0.46, 0.75, 1.02.

the eyes should compensate for any target motion not tracked by the head. This difference between target velocity and head velocity is called head slip below. The lag or lead of the eyes was related to head slip. For each analysis, the peak correlation, its time difference, and the corresponding position or velocity shifts were determined. The timing estimates are insensitive to possible calibration errors of the EOG.

Statistical methods

Owing to missing data, a straight repeated measurement model could not be applied to the whole age range. Two different procedures were instead applied. First, a general linear model was used with age as between-subject variable and conditions as within-subject variable (split-plot). Although the split-plot analysis does not take advantage of the fact that the same subject was studied at more than one age level, it is able to include all the different experimental sessions (see Table 1). In addition, a repeated measurement model was used to test changes between age levels. Thus, between 2 and 3 months of age changes could be tested on nine subjects (for time coincidence eight subjects) and between 3 and 5 months on four subjects. Missing values were substituted with the total mean in all the analyses. SYSTAT was used for ANOVA tests.

TABLE 2. Mean frequency (n/sec) and mean amplitude of the saccades (deg) for the different conditions and ages studied

		Sinus				Triangular			
		0.2 Hz		0.4 Hz		0.2 Hz		0.4 Hz	
		LA	HA	LA	HA	LA	HA	LA	HA
2 mo.	Freq.	1.3	1.7	1.6	2.2	1.3	1.8	1.9	2.2
	Ampl.	2.2	3.6	4.2	7.8	2.1	4.1	3.7	7.9
3 mo.	Freq.	0.8	1.3	1.2	1.7	1.0	1.4	1.6	2.1
	Ampl.	2.4	2.5	2.4	6.0	1.8	3.0	3.3	6.0
5 mo.	Freq.	1.1	1.4	1.3	2.2	1.3	1.7	1.7	3.0
	Ampl.	1.4	3.0	2.8	5.1	1.9	3.2	3.9	6.3

LA, low amplitude target motion; HA, high amplitude target motion.

RESULTS

Attention

One of the most clear developmental transitions observed in this study was a dramatic change in attention. At 2 and 3 months of age, the infants looked devotedly at the moving target and only two trials at each of these ages had to be disregarded due to inattention. At 5 months of age, however, there were hardly any trials where the infants did not look away at least once. The look-aways

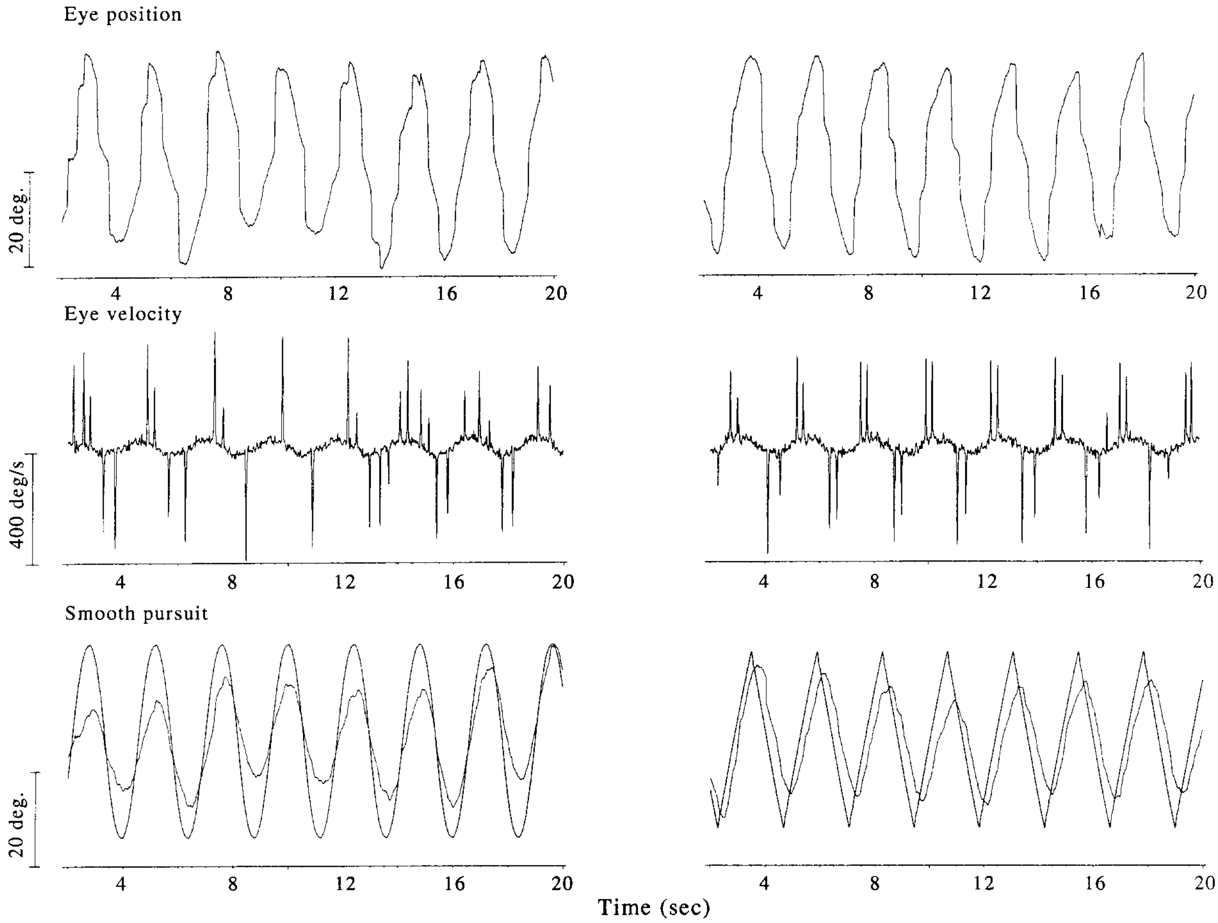

FIGURE 6. Examples of position and velocity profiles of composite eye movements, and the smooth pursuit position profiles after the saccades had been removed. Both examples are from a single 3-month-old subject and both target motions were high amplitude, 0.4 Hz. The position gains of the eye movements were 0.94 and 1.34 for the sinusoidal and the triangular motions, respectively. Corresponding figures for the smooth pursuit components were 0.52 and 0.71. It can be seen that the smooth pursuit tracking of the triangular motion had a substantial time lag (max $r = 0.97$ at a lag of 277 msec) while it was more modest for the sinusoidal motion (max $r = 0.96$ at a lag of 80 msec).

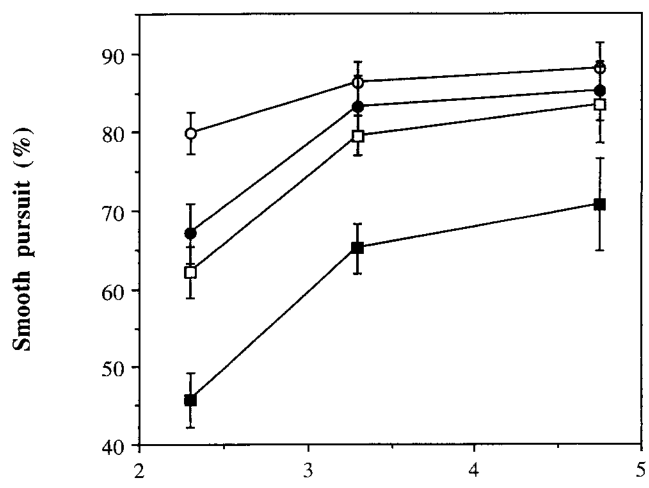

FIGURE 7. Mean and SEM of percentage gain of smooth pursuit for the different amplitudes and frequencies at the different age levels (circles = 0.2 Hz, squares = 0.4 Hz, open = 10 deg amplitude, filled = 20 deg amplitude).

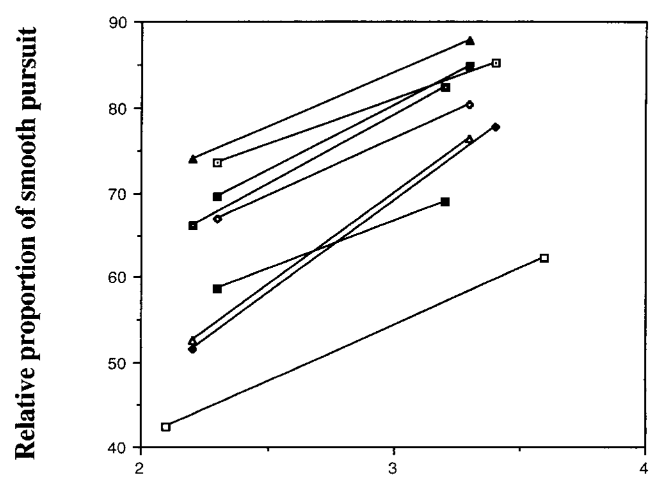

FIGURE 8. Mean percentage smooth pursuit gain for individual subjects at 2 and 3 months of age.

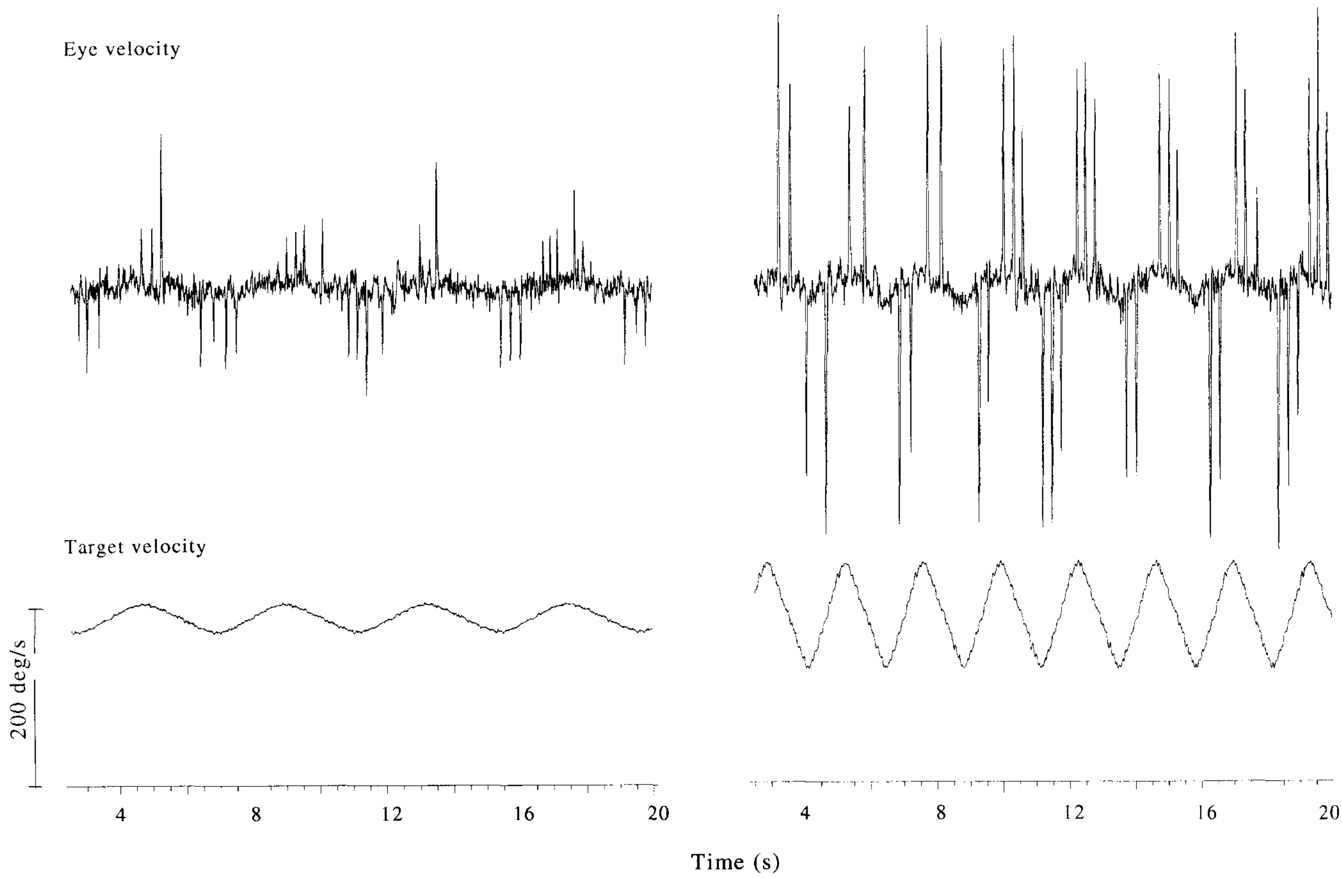

FIGURE 9. The eye velocities of a 2-month-old subject for the 0.2 Hz low amplitude and 0.4 Hz high amplitude target motions. Target velocity is also shown as a reference.

TABLE 3. Mean maximum cross-correlation coefficients and corresponding time lags (msec) of smooth pursuit velocity relative to head slip for the different conditions and ages studied

		Sinus				Triangular			
		0.2 Hz		0.4 Hz		0.2 Hz		0.4 Hz	
		LA	HA	LA	HA	LA	HA	LA	HA
2 mo.	Time	−72	−10	−100	−116	−220	−263	−228	−260
	Corr	0.45	0.62	0.61	0.65	0.37	0.53	0.51	0.56
3 mo.	Time	−29	−9	−90	−61	−198	−214	−241	−242
	Corr	0.54	0.75	0.75	0.85	0.42	0.61	0.64	0.66
5 mo.	Time	−10	212	20	114	−124	−88	−120	31
	Corr	0.44	0.53	0.67	0.79	0.37	0.53	0.60	0.52

LA, low amplitude; HA, high amplitude.

were not due to disinterest. They were generally of short durations, as if the infants merely wanted to check what else was going on around them. However, if this happened too often the trial could not be analysed. Thirty-eight individual trials had to be disregarded and 5/11 infants had to be excluded at this age level (less than five acceptable trials).

Gains

Infants were able to track the target at all ages and all conditions, engaging both head and eyes. The average gains of gaze, eyes and head movements for the different ages studied can be seen in Fig. 3. Examples of good pursuit tracking can be seen in Figs 4 and 5.

Gaze. At all ages, the infants followed the moving target closely with head and eye movements. This can be seen in Fig. 3. The mean increase in gaze gain between 2 and 3 months of age was statistically significant ($F(1,8) = 6.606$, $P < 0.05$). The split plot analysis showed main effects of all three experimental variables (see Table 1). There were also significant interactions between frequency and amplitude and between motion type and frequency. At 0.4 Hz, the triangular motion gave rise to higher gains than the sinusoidal one and the gains

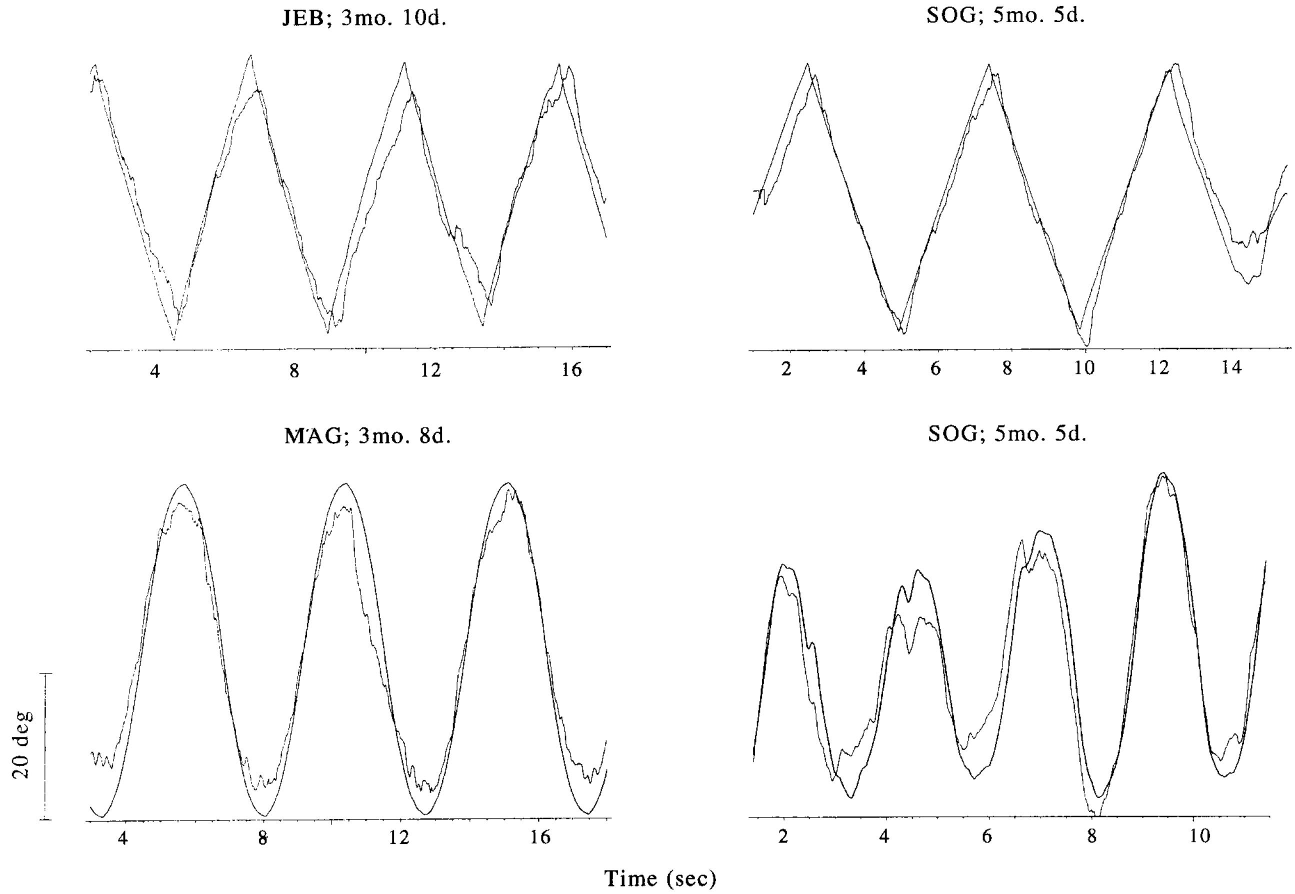

FIGURE 10. The smooth pursuit position superimposed on the difference between target and head positions for parts of the examples of sinusoidal and triangular motions shown in Figs 5 and 6. For the examples of sinusoidal motion, the smooth pursuit was leading the target by 52 msec ($r = 0.99$) for MAG at 3 months, and by 62 msec ($r = 0.97$) for SOG at 5 months. For the examples of triangular motion, the smooth pursuit was lagging the target by 150 msec ($r = 0.98$) for JEB at 3 months, and by 88 msec ($r = 0.98$) for SOG at 5 months.

were higher at 10 than at 20 deg amplitude. This was due to overshooting at the turning points.

Head. On average, head gain increased significantly (see Table 1) over the age period studied and the increase was substantial between 3 and 5 months of age which can be seen in Fig. 3. This is definitely not just a trend towards more head movements in a general sense. The Fourier analyses showed that the increase in head movement only concerned the frequency of the target motion. The trend was very different for different subjects. At 5 months of age, one subject had a mean head gain of 1.14 while another had a gain of just 0.06. The split-plot analysis of head gains showed a main effect of frequency and amplitude but no effect of motion type. There is also an interaction between age and amplitude on head gain ($F(2,23) = 13.83$, $P < 0.001$) such that the higher motion amplitude gave rise to lower gains at 2 and 3 months but higher gains at 5 months of age.

Eye. As the gain of head movement increased over age, the gain of eye movements decreased (see Table 1). As was the case for gaze, there were main effects of frequency amplitude as well as of motion type on gain of eye movements. No interactions were significant, however.

Smooth pursuit

Figure 6 shows two examples of composite eye movements, their velocity profiles with the saccadic peaks, and the derived smooth pursuit records. Repeated measurement analysis of the proportion of smooth pursuit, i.e., the ratio of eye gain with and without saccades, for the 2–3 month period showed a substantial increase with age ($F(1,8) = 84.13$, $P < 0.001$) but the difference between 3 and 5 months of age was less uniform and not statistically significant. Furthermore, the increase with age between 2 and 3 months was found to be dependent on the frequency ($F(1,8) = 16.32$, $P < 0.01$) and amplitude ($F(1,8) = 5.765$, $P < 0.01$) of the motion. This is illustrated in Fig. 7. As can be seen from Fig. 7, the motion with low amplitude and frequency elicited a high proportion of smooth pursuit already for the 2-month-olds. The split-plot analysis showed a main effect of amplitude and frequency (see Table 1). A higher proportion of smooth pursuit at the lower amplitude and frequency was found. There was also an interaction between amplitude and frequency such that the effect of frequency was more pronounced at the higher amplitude. Finally, there was an interaction between motion type and frequency. At 0.2 Hz, motion

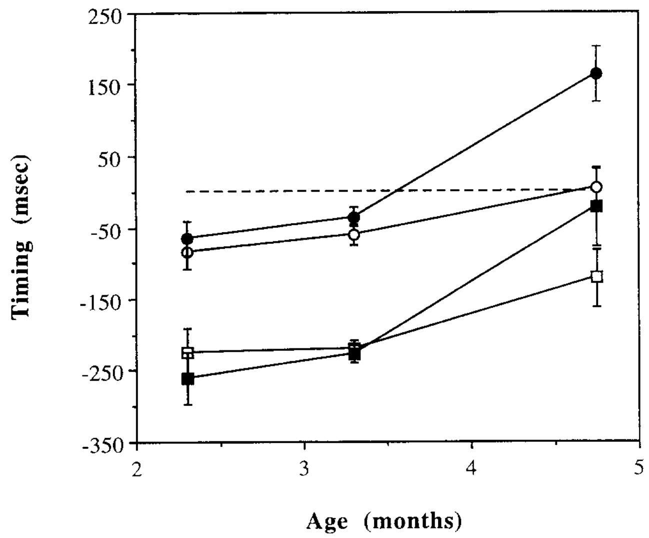

FIGURE 11. Mean and SEM of velocity time shifts between the smooth pursuit and head slip for the different motion functions and amplitudes at the different age levels. Positive values correspond to a lead for the eyes (circles = sinus, squares = triangular, open = 10 deg amplitude, filled = 20 deg amplitude).

type did not matter much but at 0.4 Hz the sinusoidal motion elicited more smooth pursuit than the triangular motion.

The proportion of smooth pursuit varied substantially between subjects but the individual differences were quite predictable from 2–3 months of age. The correlation between individual results at these two ages was 0.89. This is seen in Fig. 8.

Saccadic tracking

Frequency of saccades. Saccades occurred very regularly and often came in bursts at the higher velocity parts of the motion as shown in Fig. 9. The number of saccades in the different conditions at the different age levels studied can be seen in Table 2. The split-plot analysis did not show any change with age and neither did the repeated measurement analysis. No interactions between age and experimental variables were found. There were main effects of motion type, amplitude, and frequency (see Table 1). The triangular motion elicited more saccades than the sinusoidal one. Number of saccades increased with both amplitude and frequency.

Systematic differences between subjects were found for the 2 and 3-month-olds but they were not stable over this age range. For one subject, the saccade frequency decreased from 3.35 saccades/sec at 2 months to 1.04 at 3 months of age, while for another subject it increased from 0.93 at 2 months to 2.39 at 3 months of age.

Amplitude of saccades. Table 2 shows how amplitude of saccades were scaled to the velocity of the target. Average amplitude of saccades decreased significantly between 2 and 3 months ($F(1,8) = 7.91$, $P < 0.05$) but not between 3 and 5 months of age. There were no effects of motion type but substantial effects of motion frequency and amplitude. Finally, there was a significant interaction between amplitude and frequency (Table 1). Essentially, saccadic amplitude varied as a function of target velocity.

Time coincidence relationships

Figure 10 shows examples of the timing of smooth pursuit for 3-month-olds and 5-month-olds tracking sinusoidal and triangular motions.

*Smooth pursuit–head slip.** Table 3 shows the average cross-correlations and the corresponding time shifts for the different conditions. The lag was relatively constant between 2 and 3 months of age and decreased significantly between 3 and 5 months of age ($F(1,3) = 12.55$, $P < 0.05$). At 5 months, the smooth pursuit eye velocity was actually leading the head slip, on average.

The split-plot analysis showed an effect of motion type (see Table 1). The lag was significantly smaller for the sinusoidal than for the triangular motion. There was also a main effect of motion amplitude and an interaction between age and amplitude ($F(2,22) = 9.82$, $P < 0.001$). At 2 and 3 months of age amplitude had no effect but at 5 months of age the high amplitude motions were better predicted than the low amplitude motions. For the high amplitude motions the eyes were leading with 70 msec on average and for low amplitude motions they were lagging with 60 msec. This effect is shown in Fig. 11.

Head–target. The only significant effect on head velocity lag was the difference between sinusoidal motion and triangular motions for the measurements made at 2 and 3 months ($F(1,7) = 23.58$, $P < 0.01$). For this period the average head lag was 221 msec for sinusoidal motion and 294 msec for triangular motion. Head velocity lagged target velocity considerably at all three ages, or on average over all conditions, with 250, 266 and 337 msec at 2, 3 and 5 months of age, respectively. Average maximum correlation between head velocity and target velocity was 0.42, 0.37, and 0.53 at 2, 3 and 5 months of age, respectively.

DISCUSSION

Smooth pursuit

The development of smooth pursuit was found to be progressing well at 2 months of age. All the infants studied displayed some smooth eye tracking at that age although the relative amount varied between subjects. The gain of smooth pursuit improved substantially between 2 and 3 months of age. Although there was great consistency between the different subjects with respect to this improvement, this development was found to be highly dependent on the task. While the proportion of smooth pursuit was close to a ceiling level in the slowest condition already at 2 months of age, it was much lower in the fastest condition and increased considerably up to 3 months (see Fig. 7). In adults it has earlier been shown that smooth pursuit gain decreases when the frequency or the amplitude of the target increases (e.g.

*Difference between target velocity and head velocity.

Lisberger *et al.*, 1981; Pola & Wyatt, 1991). This points to the importance of defining the development of abilities in relation to the tasks to which they are going to be applied.

The improved timing with age of the smooth pursuit and the difference between the sinusoidal and the triangular motions revealed facts about developing mechanisms for prediction. At 2 and 3 months, large differences in the time lags between the two motion types were found. These differences can be accounted for by a velocity-based local extrapolation process functioning at this age period. Such a process allows for prediction of the continuous sinusoidal motion but not for the abruptly changing triangular motion. The magnitude of the triangular motion time lags also indicates that they are nonpredictive.

The time lags for the sinusoidal motions at 2 and 3 months are comparable to those obtained by von Hofsten & Rosander (1996) for a sinusoidally moving wide angle stimulus. In that study, a group of 1-month-old infants showed a time lag of around 200 msec, while groups of 2- and 3-month-olds had time lags of 105 and 70 msec, respectively. Thus, it seems that the ability to extrapolate a sinusoidal motion emerges some time between 1 and 2 months of age. The time lags are comparable to those obtained from adult experiments on visual tracking of pseudo-random motions where only local extrapolation processes are conceivable. Bahill & McDonald (1983) found a time lag for such motion of 95 msec. Inspection of the smooth tracking components of eye trackings indicate that higher-order motion characteristics are evaluated as well (e.g. Krauzlis & Lisberger, 1994).

The neural basis of extrapolation is not yet well known, but there have been several suggestions as to the kind of mechanisms responsible. The more simple extrapolation behaviour could easily be accounted for by a low-pass filtering process (Stark, 1968). A more advanced version of such a model has been suggested by Neilson *et al.* (1993). Prediction in this model is achieved by adaptive neural filters that automatically tune their synaptic weights to form moving average statistical models of the sensory signals. These adaptive filters generate predictions of future values of sensory signals by tuning themselves to minimise the variance of prediction errors. Other kinds of models have been presented by Miall *et al.* (1993) in which the time problem and the spatial problem of tracking are treated separately and by Barnes (1993) in which head and eye velocity estimates are released in a predictive manner under the control of a periodicity estimator. Several of these models (see e.g. Miall *et al.*, 1993; Kawato & Gomi, 1992) assume that the cerebellum is a crucial part of the extrapolation process. This is quite possible in the light of the present results. At birth, the human cerebellar cortex has a well established architecture with, for example, all Purkinje cells present (Rakic & Sidman, 1970).

At 5 months the eye movements were clearly more predictive than at the younger ages. The eyes were actually leading the sinusoidal motion and were only slightly behind the triangular motion. As the velocity of the triangular motion cannot be extrapolated at the turning points by a local process, the improvement of tracking can only be explained in terms of prediction of its periodicity. The more advanced extrapolation mechanisms presented by, for instance, Neilson *et al.* (1993) could, in principle, handle such global prediction.

However, it is also possible that the infants formed expectations of where or when the target would switch direction. This suggestion is in line with results obtained by Haith and associates (Haith *et al.*, 1988; Canfield & Haith, 1991; Wentworth & Haith, 1992). They demonstrated that infants will predict where and when the next picture in a left–right sequence is going to be shown, by moving the eyes there just before the picture appeared. Whether an adaptive filter model or a more cognitive-based prediction applies to the improvement between 3 and 5 months of age is beyond the scope of the experiments reported.

The head lagged the target by at least a quarter of a second on average. This lag did not diminish with age, which implies that the prediction mechanism behind smooth pursuit eye movements does not automatically apply to head tracking. However, the coupling between head and eye movements seems very fundamental. Together they determined the change in gaze and whatever the amount of head movements recruited, the gain of the gaze was close to 1.

Saccades

At 5 months, the relative proportion of saccades was actually quite adult-like. For the sinusoidal motion, saccades accounted for 6% of the gain at 0.2 Hz and 14% of the gain at 0.4 Hz. These values may be compared to those obtained by Collewijn & Tamminga (1984). The interpolated proportion of saccades for 0.2 and 0.4 Hz in their study were 10% and 25%, respectively. It should be noted, however, that their target was much smaller (7′ of arc) than the 10 deg in the present study.

Amplitude of saccades was found to be related to the velocity of the target at all ages studied. This is different from the saccades involved in redirecting gaze. In that situation, all saccades performed by young infants were found to be of similar size (Salapatek *et al.*, 1980). The present result shows that this is not the case because they cannot master saccades of various amplitudes. Large saccades are produced in a situation where they are more crucial, as in the tracking of a fast target.

The smooth component of the eye movements lagged the target less than the eye movements with saccades included. This indicates that the saccades constitute a delay in the tracking. This seems logical since the saccades are reactions to retinal displacements. The same is valid for adult tracking (Bahill & McDonald, 1983).

Smooth pursuit and OKR

In the present study, the gaze gains were higher than those in von Hofsten & Rosander (1996), in which case the centrally positioned target was surrounded by a large grating pattern covering the whole visual field. They found that tracking was still incomplete at 3 months of age with a gaze gain of around 0.70. This indicates that a target of limited size surrounded by a homogeneous visual field is a better target for tracking than a wide angle stimulus even for a 2-month-old infant. Earlier research on rhesus monkeys by Miles *et al.* (1986) showed that the gain of the tracking decreased for visual angles above 20 deg. They argued that a system compensating for body locomotion in a natural environment should optimally react to rather local optical motion, as the amount of optical motion is dependent on observation distance. Some recent neural findings are also in line with this viewpoint (Komatsu & Wurtz, 1988; Born & Totell, 1992).

In the literature on smooth tracking, a distinction between smooth pursuit and OKR is often made. We do not make this distinction. It is difficult to classify the present results in terms of this terminology partly because no absolute border has been defined between these two mechanisms. The 10 deg target might be in the OKR range. However, this would imply that OKR predicts target motion in the same advanced way as smooth pursuit which weakens the arguments for two separate mechanisms. Clearly, very young infants only pursue large targets and with a large lag but this may just reflect the immaturity of one developing system. Studying the development of smooth tracking as a function of target size may shed light on this question. This is the next natural step in this series of investigations.

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