Available online at www.sciencedirect.com

SCIENCE DIRECT®

Vision Research 46 (2006) 1754–1761

Vision Research

www.elsevier.com/locate/visres

Developmental asymmetries between horizontal and vertical tracking

Helena Grönqvist *, Gustaf Gredebäck, Claes von Hofsten

Department of Psychology, Uppsala University, Box 1225, SE-75142 Uppsala, Sweden

Received 12 May 2005; received in revised form 3 November 2005

Abstract

The development of the asymmetry between horizontal and vertical eye tracking was investigated longitudinally at 5, 7, and 9 months of age. The target moved either on a 2D circular trajectory or on a vertical or horizontal 1D sinusoidal trajectory. Saccades, smooth pursuit, and head movements were measured. Vertical tracking was found to be inferior to horizontal tracking at all age levels. The results also show that the mechanisms responsible for horizontal and vertical tracking mutually influence one another in the production of 2D visual pursuit. Learning effects were observed within-trials but no transfer between trials was found.

Keywords: Visual development; Infants; Visual tracking; Vertical eye movements; 2D tracking

1. Introduction

A functional visual system requires versatile eye and head movements in both the horizontal and vertical dimensions of the visual field. Two kinds of eye movements make this possible: saccades and smooth pursuit (SP). When smooth pursuit is insufficient to track a moving target, catch-up saccades are employed to recapture it. Studies with adults and nonhuman primates have shown that SP tracking is more efficient in the horizontal than in the vertical dimension. For instance, Collewijn and Tamminga (1984) found that the horizontal tracking component was smoother than the vertical one when subjects pursued a target moving on a circular trajectory. Additional studies with both humans (Baloh, Yee, Honrubia, & Jacobson, 1988; Rottach et al., 1997) and rhesus monkeys (Kettner, Leung, & Peterson, 1996; Leung & Kettner, 1996) have replicated this general pattern of results.

The developmental origins of the horizontal–vertical tracking asymmetry are not well known. Most studies on the development of gaze tracking have presented infants with targets that move along a horizontal trajectory according to a sinusoidal velocity profile (Aslin, 1981; Dayton & Jones, 1964; Phillips, Finoccio, Ong, & Fuchs, 1997; Rosander & von Hofsten, 2000, 2002; von Hofsten & Rosander, 1996, 1997). When targets move in this manner, two-month-old infants are capable of producing predictive SP. Very few studies have explored vertical and 2D tracking in human children. Takeichi et al. (2003) found that vertical SP was inferior to horizontal SP in both children and young monkeys. The children, however, were 9- and 11-years-old, and thus too old to illuminate the developmental origins of smooth pursuit in humans. Richards and Holley (1999) studied 8- to 26-week-old infants' tracking of a rectangle that moved either horizontally or vertically. They found that horizontal tracking was more mature than vertical tracking at this period of development. They also found attention to be better for horizontal motion. These results are somewhat difficult to interpret, however, since the target was asymmetrical ($2_{horizontal} * 6_{vertical}$). It is therefore possible that the larger vertical extension may have induced more mature horizontal tracking.

Gredebäck, von Hofsten, and Boudreau (2002) Gredebäck, von Hofsten, Karlsson, and Aus (2005) studied infants' visual tracking of targets moving on a circular trajectory. Gredebäck et al. (2002) found that the horizontal component of 9-month-old infants' tracking of such targets

* Corresponding author.
E-mail address: helena.gronqvist@psyk.uu.se (H. Grönqvist).

0042-6989/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2005.11.007

was more mature than the vertical component. More specifically, the horizontal component was predictive and centered on the target, whereas the vertical component lagged behind the target and displayed higher variability of gain. This result was replicated and extended in a longitudinal study where 6- to 12-month-old infants were presented with objects moving on circular trajectories (Gredebäck et al., 2005). Both the horizontal and vertical components of SP were predictive by 8 months of age when the targets moved at 10 °/s. At higher velocities (20 °/s), the vertical component consistently lagged behind at all ages tested, except at 12 months. Gredebäck et al. (2005) also found that the horizontal component of infants' circular tracking was less mature than expected from earlier studies of their performance on 1D sinusoidal motion (von Hofsten & Rosander, 1997). One possible reason for this effect is that vertical and horizontal tracking do not function independently of each other. The horizontal component of circular tracking could be negatively affected by its association with the vertical component (Leung & Kettner, 1996). Another possible reason for this asymmetry, is that circular tracking is more difficult than linear tracking and that this negatively affects both the vertical and horizontal tracking components (Rottach et al., 1997).

The aim of the present study was to clarify further the nature of the horizontal–vertical tracking asymmetry in human infants by comparing the tracking of 1D vertical and horizontal motion to the vertical and horizontal tracking components of 2D circular motion. Is there a dependent relationship between the vertical and horizontal components in 2D visual tracking or do they function independently? The present study tested these alternatives by comparing infants' ability to track a target that moved either on a 2D circular trajectory or on a vertical or horizontal 1D sinusoidal trajectory. The gain and timing of SP and saccades, as well as the infants' ability to center the gaze on the moving object were calculated for each trial.

Another aim of the present study was to evaluate development and learning effects. Learning was evaluated on three different time scales: the change in performance within each trial, the change in performance between two experimental sessions conducted on the same day, and the change in performance between experimental sessions conducted on two consecutive days. The infants were followed longitudinally from 5 to 9 months of age. This made it possible to evaluate developmental changes during this age period. This age span has proven to be an interesting period in the development of horizontal and vertical eye movements (Gredebäck et al., 2005).

2. Methods

2.1. Participants

Ten healthy full-term infants (six girls and four boys) were studied longitudinally at 5, 7, and 9 months of age (average age on the first of the two consecutive days was 157 ± 7, 214 ± 10, and 274 ± 5 days). The infants were recruited from birth records in a metropolitan area. Families received a letter describing the research with a reply form they could use to indicate their interest in participating. Families that replied were contacted for an appointment. The volunteers were primarily from middle-class families. At each visit, the families received a choice of two movie tickets or eight local bus tickets for their participation (value approximately 16€). The study was approved by the ethics committee of Uppsala University and accorded with the ethical standards specified in the 1964 Declaration of Helsinki.

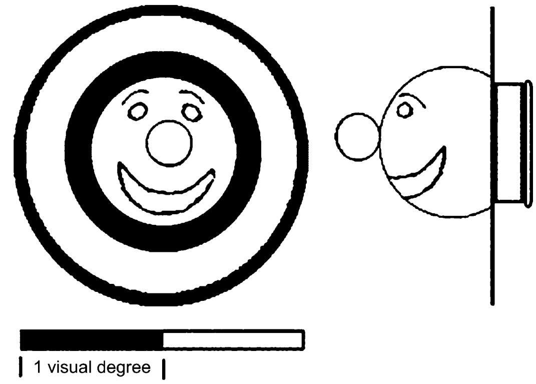

Fig. 1. The stimulus seen from the front and from the side.

2.2. Apparatus and visual stimuli

Gaze direction was measured with a remote ASL 504 eye tracker (Bedford MA). The ASL is a remote tracking system that calculates gaze using the reflection of a near infrared light from the cornea and pupil of one eye with a sampling rate of 50 Hz[1]. The performance of the right eye was measured. Head position was recorded with a magnetic tracker, Flock of Birds (Ascension, Burlington, VT). This device has a Mini Bird head tracker that provides head position coordinates so that the ASL pan/tilt camera can reconnect to the eye in case of rapid head movements (see Gredebäck et al., 2002).

The testing apparatus consisted of a target (a 3D happy face with a radius measuring 1 visual degree, see Fig. 1) that moved on a 100×100 cm vertical surface. Two orthogonally coupled servomotors were used to control the movement of a magnet on the back of the vertical surface. Another magnet was attached to the base of the target. The attraction of the two magnets supported the target's position on the surface and enabled the target to move along motion paths specified by a PC connected to the apparatus.

The display was situated on one side of a semi-enclosed room. The infant sat in an infant car seat placed on the lap of a parent facing the apparatus at a distance of about 215 ± 10 cm. A special stimulus consisting of a small face with a red LED in the forehead was used to calibrate the ASL. The stimulus was placed on the top of a rod that was manually manipulated by the experimenter. The LED was controlled by a switch on the rod's handle; a small bell behind the face made noise when the rod was rattled. The radius of the calibration stimulus measured 0.5° visual angle. During calibration, the infants' gaze was attracted to the desired positions on the vertical surface by blinking the light and rattling the bell. When the infant fixated the desired position, the experimenter pressed the calibration button.

2.3. Procedure

On the first visit to the baby lab, parents were informed of the study and signed a consent form. Two experimenters conducted the experiment. During the experiment, the infant wore a cap onto which the Mini Bird head tracker was attached above the right eye. The session began with a

[1] Adult precision 0.5°, accuracy <1°.

calibration procedure in which one experimenter moved the calibration stimulus to each of two predefined positions in front of the screen (upper left corner and lower right corner). The calibration was assessed by moving the calibration stimulus to several different positions on the screen, while at the same time measuring the gaze with the eye tracker. If the recorded gaze position did not remain stable within the area covered by the calibration stimulus, a new calibration was conducted. Calibration usually lasted between 1 and 5 min.

During the experiment, the 3D happy face was used as the target. It performed one of three different kinds of motion: a continuous circular motion with constant speed, a repetitive back-and-forth sinusoidal horizontal motion, and a repetitive sinusoidal back-and-forth vertical motion, (see Fig. 2). All motions had a maximal extension of 11° visual angle. A circular motion can be decomposed into one horizontal and one vertical sinusoidal component, and hence be compared to the 1D trajectories. Two frequencies were used, 0.2 or 0.4 Hz, corresponding to a maximum velocity of 6.9 and 13.8 °/s, respectively. These frequencies were chosen because they were identical to those used by Gredebäck et al. (2005). They are also comparable to the frequencies used by von Hofsten and Rosander (1997) and Rosander and von Hofsten (2000, 2002). Each condition was presented twice. The circular conditions were presented once clockwise and once counter-clockwise. Thus, the whole experiment consisted of 12 trials. The order of presentation was randomized for each infant.

Each trial lasted 20 s and in between trials there was a 5–10 s pause. During this pause, one experimenter prepared the next motion, while the other interacted with the infant. The trials were infant-paced and started when the infant attended to the stimulus. During the experiment, the parent was encouraged to sing or talk to the infant if this made the infant more relaxed. If the infant lost concentration, a small break was taken. If the infant was inattentive during a trial, that trial was presented again at the end of the experiment, if possible. The entire experiment lasted 15–25 min, depending on the state of the infant. The stimuli were shown twice at each visit, in two randomized orders. The same procedure was repeated on two consecutive days at each age level.

2.4. Data analysis

For a trial to be included in the analysis, the infant had to track the target continuously over at least one full cycle with less than 1 s of disengagement. This criterion was fulfilled for 62% of the trials in the 0.4 Hz condition and 37% of the trials in the 0.2 Hz condition. The difference was primarily a function of the length of the cycle in each condition. In the 0.2 Hz condition a full cycle took 5 s to complete, while in the 0.4 Hz condition it took 2.5 s. Thus, to be included in the data analysis, infants were required to track the target for twice the time in the 0.2 Hz condition compared to 0.4 Hz condition. Often infants started to track the object in the 0.2 Hz condition, but then disengaged before a full cycle was completed. They sometimes looked back at the target before the cycle ended, but the time away was usually too long for interpolation. Due to the extensive amount of missing data in the 0.2 Hz condition, we confined our analysis to the 0.4 Hz condition. For each trial, the largest segment of continuous tracking with no more than 1.0 s of interruption was analyzed. If the infant looked away or lost concentration for less than 1.0 s, the data was linearly interpolated over this time. Altogether 2.5% of the data were interpolated in this way. Data was filtered using a 4-sample-mean-filter to reduce high frequency noise. This filter was chosen because it reduced noise well without serious impairment of the ability to identify saccades. In order for a participant to be included in the analysis the infant had to have over 50% successful trials.

The 2D circular data were divided into a horizontal and a vertical component that were separately analyzed. Whether the circular motions were run clockwise or counter-clockwise had no systematic effect on the results and their analyses were therefore collapsed. Gaze and its three motion type components; saccades, smooth pursuit (SP), and head movements were analyzed separately. Gaze direction was measured by the eye tracker and head movements by the head tracker. Saccades were defined as eye movements faster than 50 °/s (visual angle). They were extracted and stored separately. SP was calculated by removing saccades and head movements from gaze data.

Gain was computed for all three motion components plus gaze, calculating the relative amplitude of the object and eye velocities. Timing in milliseconds was calculated as the cross correlation between the object and the eye, head, and gaze velocities. Predictive tracking was assumed to operate when the average timing did not lag more than 200 ms for saccades (Engel, Anderson, & Soechting, 1999; Rosander & von Hofsten, 2004) and 125 ms for SP (Robinson, 1965; Rosander & von Hofsten, 2002). Because the head movements had small gains (average 3%) and were relatively uncorrelated with the object motion, they were not further analyzed. The average distance (RMS) of the visual angle between gaze and the center of the object was also calculated using root mean square for each trial. Timing and RMS give somewhat different estimates of performance. If the timing of gaze is unstable and half the time lags the object and half the time leads it, the average timing would indicate that the eye is on the object. RMS reflects how far, on the average, gaze is from the object, irrespective of whether it leads or lags it. Repeated mea-

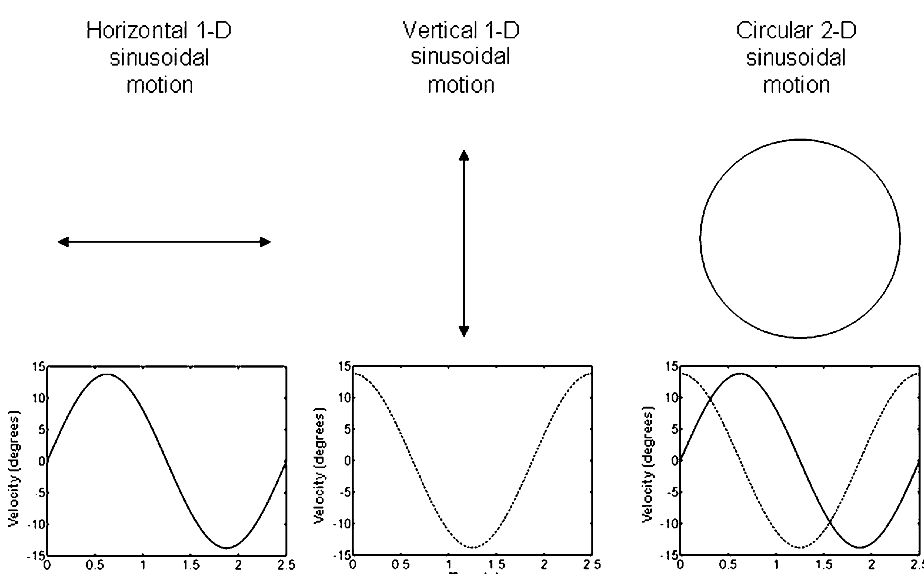

Fig. 2. The different object motions used in the experiment. The top row of figures shows the trajectories of the object. The bottom row shows the velocity profile of the motion.

surement ANOVAs were performed on gain, timing, and RMS averaged over the two trials of a session and two sessions of each age. Infant data is rarely complete since it is impossible to instruct the subjects. Therefore the data were collapsed in order to get a fair data matrix. Every data point in the ANOVA was thus the average of 1–4 measurements. This merged data file contained 4.7% missing data items which were replaced by the condition means. The independent variables in the ANOVA were age (5, 7, and 9 months), one- or two-dimensional trajectories (hereafter referred to as 1D/2D), and orientation of the currently analyzed component (horizontal and vertical, hereafter refereed to as H/V). Significant effects were pair-wise post hoc tested using Bonferroni adjustment. Post hoc tests for age had $k = 3$, interaction post hoc tests for dimension $*$ orientation had $k = 6$, and age $*$ dimension and age $*$ orientation had $k = 15$.

For each trial, linear regressions were calculated between RMS and time. A negative regression means that RMS decreases over time, indicating within-trial learning. To evaluate if the regression was positive more often than negative, a binomial test was performed.

To examine learning effects between the first and the second presentations in a session, data from the first and the second day were merged for each movement and subject. The difference in gain and timing of gaze, and saccades in addition to RMS of gaze was then tested for each infant (Student paired t test). To examine learning effects between days, the variables for the first and second presentations were similarly merged and tested (Student paired t test).

3. Results

Three infants were excluded from the study. Two infants did not pass the 50% successful trial criterion for inclusion and one family moved out of town. Thus, seven subjects were included in the analyses.

3.1. Gain

As shown in Fig. 3, infants tracked the target with velocities equal to or exceeding the velocity of the target. The minimum average gain of gaze (1.06) was measured for the horizontal component when infants tracked circular trajectories at 7 months of age, whereas the maximum average gain of gaze (1.22) was measured for vertical trajectories at 5 months of age. No significant effects of condition or age were found for gaze gain.

Each component of gaze contributed a different amount to the overall tracking (Fig. 3). No age effects were found ($p > 0.10$). Averaged over the different age groups and conditions, SP contributed to 63% of the gaze gain, whereas saccades were responsible for 34%.

Gain of SP was higher during 1D ($M = 0.76$) than during 2D ($M = 0.69$) tracking; $F(1,6) = 36.19, p < 0.01, \eta^2 = 0.858$. In addition, gain of SP was found to be higher for horizontal ($M = 0.82$) than vertical ($M = 0.63$) trajectories; $F(1,6) = 107.45, p < 0.0001, \eta^2 = 0.947$. No age effects ($p > 0.2$) or interaction effects between 1D/2D and H/V movements ($p > 0.7$) were found.

Saccades and SP supplemented each other such that lower gain of SP corresponded to higher saccade gain. In other words, saccades were negatively correlated with SP, $r(82) = -0.77$, $p < 0.01$. Thus, because SP had higher horizontal gains, saccades contributed less to the tracking of those motions ($M = 0.29$) than to the tracking of vertical

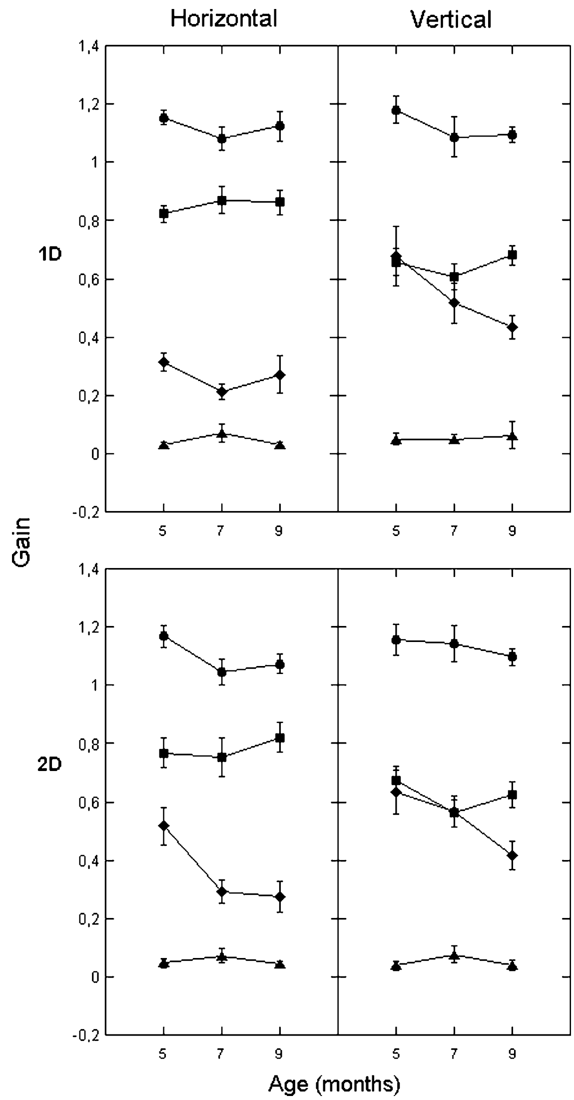

Fig. 3. Gain of gaze and its components SP, saccades, and head movement, plotted as a function of age. Separate plots are shown for the 1D and 2D motions and the vertical and horizontal. Filled circles represent gaze, filled squares SP, filled diamonds saccades, and filled triangles head.

motions ($M = 0.48$); $F(1,6) = 15.99$, $p < .05$, $\eta^2 = 0.727$. Other effects that relate to gain of saccades were not significant, with only a trend toward an age effect ($p = 0.06$). This means that dependency on saccadic tracking decreased as infants relied more on SP during continuous tracking.

3.2. Timing

The timing results can be seen in Figs. 4–6. Tracking wasz considered predictive if the average lag was less than 125 ms for SP, and less than 200 ms for saccades, as indicated by the horizontal lines.

An age effect of timing of gaze was found $F(2,12) = 21.88$, $p < 0.0001$, $\eta^2 = 0.785$. From 5 to 7 months of age, timing of gaze did not improve significantly. However, between 7 and 9 months of age the gaze lag decreased by almost 50 ms ($p < 0.001$). In addition, over all ages, the horizontal component

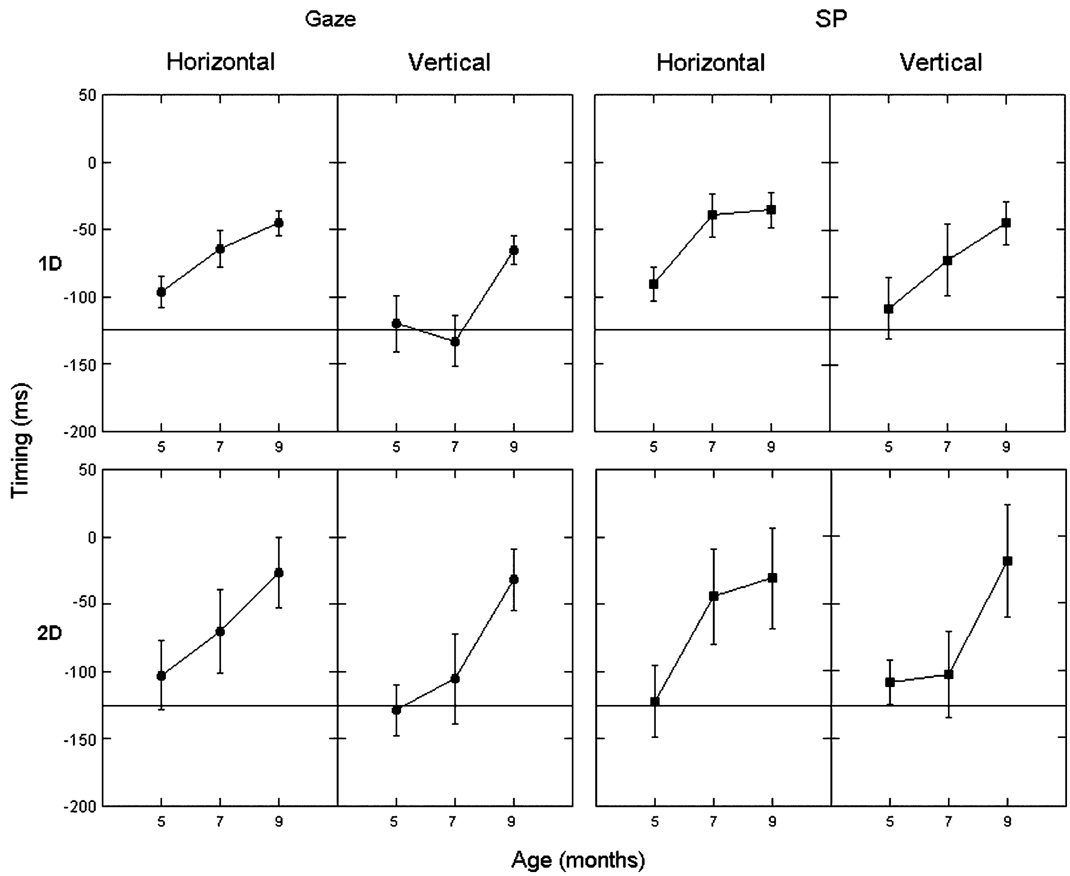

Fig. 4. Timing of gaze (filled circles) and SP (filled squares) plotted separately as a function of age. The eye movements are predictive when they are above the cut off line at −125 ms. Error bars represent StdE.

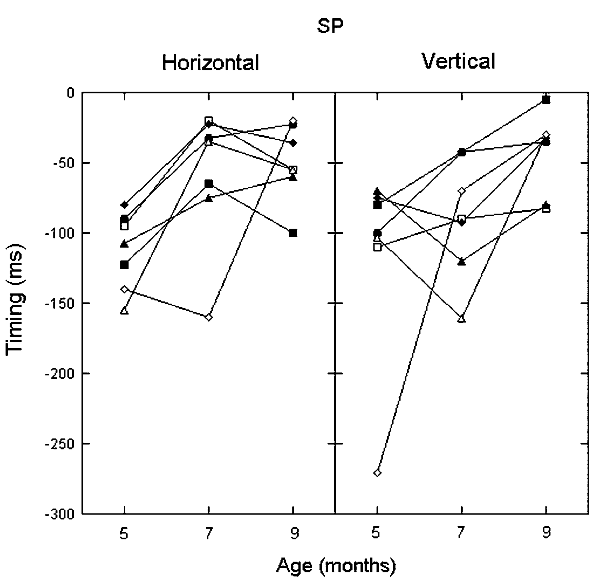

Fig. 5. Timing of SP for individual subjects plotted as a function of age. The different symbols denote the different subjects.

of gaze lagged less ($M = -71$ ms) than the vertical component ($M = -106$ ms); $F(1,6) = 17.64$, $p < .01$, $\eta^2 = 0.746$.

Fig. 4 illustrates that infants are most proficient at horizontal tracking. The average lag is less than the 125 ms threshold at all ages. Performance was less good when infants tracked the objects moving on the vertical trajectories. Under those conditions infant gaze tracking is not consistently predictive until 9 months of age.

On average horizontal SP is predictive at all ages and in response to all conditions (see Fig. 4). There was a significant improvement with age, $F(2,12) = 11.3$, $p < 0.005$, $\eta^2 = 0.653$. A post hoc test showed that the improvement was between 5 and 7 months of age ($p < 0.05$). There was also an significant interaction between 1D/2D and orientation (H/V), $F(1,6) = 7.14$, $p < 0.05$, $\eta^2 = 0.543$. Two-dimensional trajectories had a more negative effect on vertical than on horizontal tracking.

The individual differences were quite consistent ($F(1,6) = 142.16$, $p < 0.0001$, $\eta^2 = 0.96$). Fig. 5 shows that it is primarily one subject who had difficulties with predicting the motion of the objects. This subject lagged both when tracking the horizontally and the vertically moving objects. As the general patterns of results remained the same if this subject was excluded from the statistical analysis, we decided to leave the subject in the report.

Unlike gaze and SP, timing of saccades was not related to age. As can be seen in Fig. 6 there is, however, a significant difference between horizontal ($M = -78$ ms) and vertical ($M = -144$ ms) saccades; $F(1,6) = 7.65$, $p < 0.05$, $\eta^2 = 0.56$. The saccades are predictive under all conditions, but horizontal saccades are better than the vertical ones (Fig. 6). No effect of 1D/2D was found.

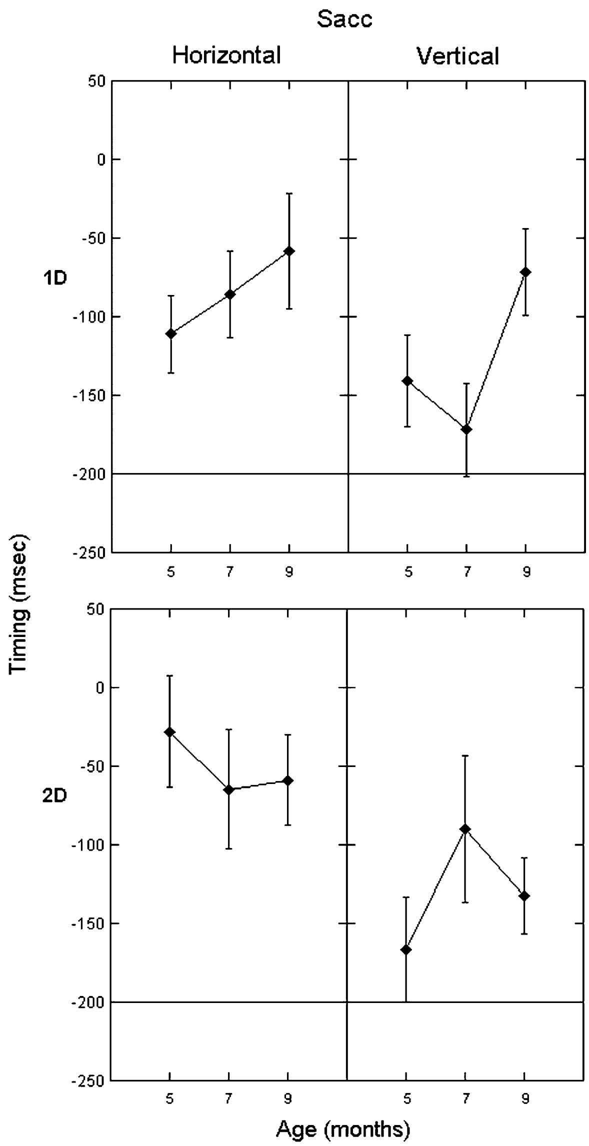

Fig. 6. Timing of saccades plotted separately for horizontal and vertical eye movements and 1D and 2D trajectories. The black line at 200 ms, denote the cut off line for predictable saccades. Error bars represent StdE.

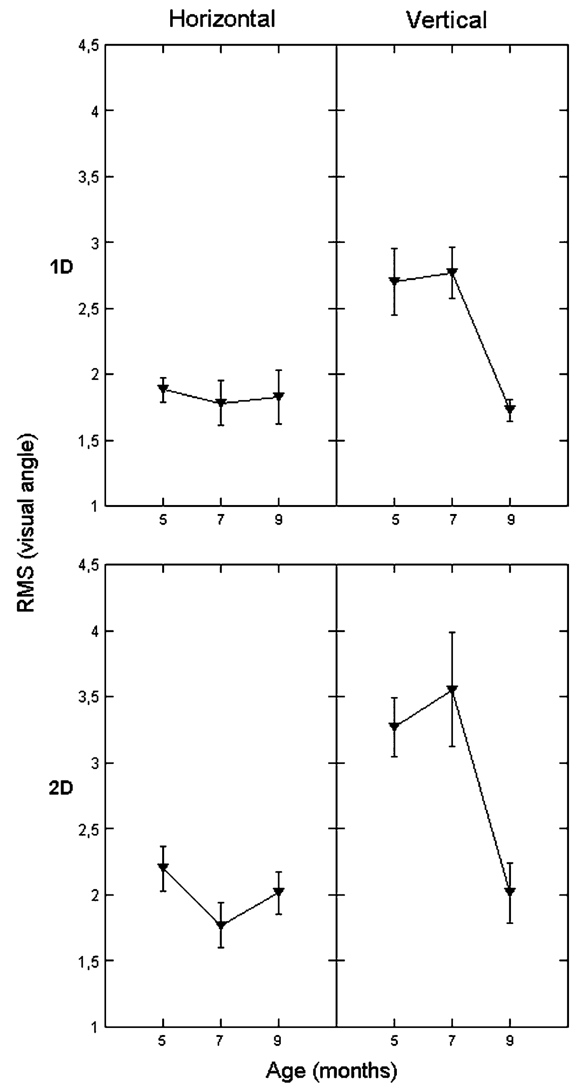

Fig. 7. RMS of gaze (distance from object center) plotted separately for horizontal and vertical eye movements and 1D and 2D trajectories. Error bars represent StdE.

3.3. RMS

The mean deviation of gaze from the center of the target decreased with age; $F(2,12) = 6.48$, $p < 0.05$, $\eta^2 = 0.519$. Post hoc tests indicated that only the difference between 5 ($M = 2.49°$) and 9 months of age ($M = 1.97°$) was significant ($p < 0.05$). In addition, horizontal gaze ($M = 1.9°$) had a smaller average deviation from the target than vertical gaze ($M = 2.6°$); $F(1,6) = 50.9$, $p < 0.0001$, $\eta^2 = 0.895$. There was also an interaction between age and orientation; $F(2,12) = 5.38$, $p < 0.05$. $\eta^2 = 0.473$. While horizontal tracking had similar average deviations at all ages, the deviation of the vertical tracking decreased with age. At 7 months the deviation of the vertical tracking was significantly higher than the deviation of the horizontal tracking, but at 9 months the deviations were comparable (see Fig. 7). Gaze also deviated less from the object during 1D ($M = 2.06°$) compared to 2D ($M = 2.46°$) tracking, $F(1,6) = 12.81$, $p < 0.05$, $\eta^2 = 0.681$ (see Fig. 7).

3.4. Learning effects

There were no differences between the first and second presentation of the same stimuli within each session, nor were there any differences between the performance on the two consecutive days of each age; measures included gain and timing of gaze, SP, and saccades, in addition to RMS of gaze. There were, however, substantial within-trial learning effects. The RMS distance for a specific trial did not remain stable, but rather decreased by an average of 1.73° over a 20 s trial. As can be seen in Table 1, this within-trial learning effect was similar for the different conditions and ages investigated.

Table 1
The average change in RMS between gaze and target center within each trial

Age	Dimension			
	1D		2D	
	Horizontal	Vertical	Horizontal	Vertical
5	−2.41	2.16	−1.02	−1.46
7	−0.26	−1.67	−1.65	−2.41
9	−2.79	−4.03	−4.71	−0.46

Negative numbers indicate a decrease in RMS over time.
Note. Data was normalized according to the length of each presentation (20 s) regardless of whether infants actually attended to the target for that amount of time or less.

4. Discussion

The results show that infants were able to track the target at all ages and in all conditions. Gaze was within the borders of the object most of the time and its gain did not change significantly across the different ages or conditions. However, the relative contribution of saccades and SP differed. Horizontal tracking had a higher proportion of SP than vertical tracking and the proportion of SP increased with age. The results also indicated differences between 1D and 2D tracking. This was primarily expressed as an increase in SP lag during 2D tracking.

4.1. Horizontal versus vertical tracking

The three measures used to assess tracking in the present study, RMS between gaze and target, gain and timing of SP, and timing of gaze and saccades, reflect different aspects of tracking efficiency. While timing and gain reflect orthogonal aspects of tracking, RMS provides an overall estimation of both these aspects. The RMS (Fig. 7) measure and the timing of gaze and SP show improvements with age. At 5 months RMS was significantly lower for horizontal than for vertical tracking, but by 9 months this difference was no longer present. For the timing measures, horizontal tracking was superior to vertical tracking, but at 9 months of age the means were similar. Gain of SP, however, differed between horizontal and vertical at all ages tested. Adults show difference in gain but not in timing between horizontal and vertical SP (Collewijn & Tamminga, 1984; Rottach et al., 1997). Thus it seems that SP gain is a more sensitive measure of tracking efficiency than either RMS or timing in both infants and adults.

Collewijn and Tamminga (1984) attribute the horizontal–vertical asymmetry in adults to the fact that most objects that are pursued in daily life move in a horizontal plane. If the difference in performance between horizontal and vertical tracking were due to experience, one would expect horizontal to improve more rapidly than vertical tracking, because horizontal motion is more common. When the horizontal component has reached its performance asymptote, vertical tracking should catch-up and, in the end, become comparable to horizontal tracking. A maturational lag could, of course, also be the reason why vertical tracking is delayed relative to horizontal tracking. The fact that horizontal tracking continues to be superior to vertical tracking in certain respects, suggests that learning cannot fully account for the developmental differences. It argues instead that different mechanisms underlie the two modes of visual tracking (Collewijn & Tamminga, 1984).

4.2. 1D and 2D tracking

The results show that infants' tracking of 1D horizontal and vertical linear motion is comparable to 2D circular tracking in some respects. The gain and timing of gaze are similar and so is the timing of saccades. There are, however, some significant differences between 1D and 2D tracking. During circular tracking, infants display poorer timing, larger RMS, and lower gains than what would be expected from a linear summation of the 1D horizontal and vertical components. These results suggest that the mechanisms responsible for horizontal and vertical tracking mutually influence each other in the production of 2D visual pursuit. Similar findings have been reported in the adult and nonhuman primate literature (Leung & Kettner, 1996; Rottach et al., 1997). The vertical component seems to be more affected than the horizontal component when a second dimension is added; this is illustrated by the interaction effect in timing of SP. This indicates that the vertical component is less robust when doing more than one thing at a time in an oculomotor sense. At least at an abstract action level, the tracking is probably organized in terms of its 2D form and not as vertical and horizontal components.

4.3. Head movements

The results of the present study are different from earlier studies of visual tracking in infants with respect to the proportion of head movements in gaze tracking. von Hofsten and Rosander (1997) found that a relatively high proportion 5-month-old infants' visual tracking consisted of head movements, and von Hofsten, Feng, and Spelke (2000) von Hofsten, Vishton, Spelke, Feng, and Rosander (1998) used head tracking as the index of visual tracking in 6-month-old infants. The difference between these studies and the present one is that the earlier studies used much larger trajectories than the present study. The trajectories used by von Hofsten and Rosander (1997) were 3.5 times larger (50°) than the ones used here, while the trajectories used by von Hofsten et al. (2000, 1998) were 10 times larger (140°). Thus, it is concluded that head movements are used to expand the visual field and that the modest size of the present trajectories did not require such expansion.

4.4. Learning effects

No evidence was found in the present study for long-term learning between experimental sessions or between days. We observed only short-term learning over single trials. Sekuler and Sekuler (1993) argued that adult predictive eye movements are based on both high- and low-level representations of tracked objects. The lower-level representations refer to stimulus-driven predictions, based on the current trajectory. When infants continuously track a target that moves in a predictable manner, it is conceivable that the error term of an internal model decreases. This results in more predictive tracking as a function of time (Kowler, 1990). This type of loop is largely involved in generating predictive SP (Leight & Zee, 1999). The high-level representations are reflected in the improvements over trials or experimental sessions. Such learning was not observed in the present experiment although each condition was presented twice to the subjects within each experimental session. It is possible that it would be observed if more experience had been provided. Although, each subject participated in four experimental sessions over two consecutive days, the total exposure time to the moving objects was only 16 min.

Acknowledgments

We thank the enthusiastic parents and infants who made this study possible. We also thank Kerstin Rosander for many valuable suggestions. This study was supported by the Swedish Council for Research in the Humanities and Social Sciences.

References

Aslin, R. (1981). Development of smooth pursuit in human infants. In D. F. Fischer, R. A. Monty, & E. J. Senders (Eds.), *Eye movements: Cognition and vision perception* (pp. 31–51). Hillsdale, NJ: Erlbaum.

Baloh, R. W., Yee, R. D., Honrubia, V., & Jacobson, K. (1988). A comparison of the dynamics of horizontal and vertical smooth pursuit in normal human subjects. *Aviation, Space, and Environmental Medicine, 59*, 121–124.

Collewijn, H., & Tamminga, E. P. (1984). Human smooth and saccadic eye movements during voluntary pursuit of different target motions on different backgrounds. *Journal of Physiology, 351*, 217–250.

Dayton, G. O., & Jones, M. H. (1964). Analysis of characteristics of fixation reflex in infants by use of direct current electrooculography. *Neurology, 14*, 1152–1156.

Engel, K. C., Anderson, J. H., & Soechting, J. F. (1999). Oculomotor tracking in two dimensions. *Journal of Neurophysiology, 81*, 1597–1602.

Gredebäck, G., von Hofsten, C., & Boudreau, J. P. (2002). Infants' visual tracking of continuous circular motion under conditions of occlusion and non-occlusion. *Infant Behavior and Development, 25*, 161–182.

Gredebäck, G., von Hofsten, C., Karlsson, J., & Aus, K. (2005). The development of two-dimensional tracking: A longitudinal study of circular pursuit. *Experimental Brain Research, 163*, 204–213.

Kettner, R. E., Leung, H., & Peterson, B. M. (1996). Predictive smooth pursuit of complex two-dimensional trajectories in monkey: Component interaction. *Experimental Brain Research, 108*, 221–235.

Kowler, E. (1990). The role of visual and cognitive processes in the control of eye movements. In E. Kowler (Ed.), *Reviews of oculomotor research* (p. 40). New York, NY: Elsevier.

Leight, R. J., & Zee, D. S. (1999). *The neurology of eye movements* (3rd ed.). New York, NY: Oxford University Press.

Leung, H., & Kettner, R. E. (1996). Predictive smooth pursuit of complex two-dimensional trajectories demonstrated by perturbation responses in monkeys. *Vision Research, 37*, 1354–1374.

Phillips, J. O., Finoccio, D. V., Ong, L., & Fuchs, A. F. (1997). Smooth pursuit in 1 – 4-month-old human infants. *Vision Research, 37*, 3009–3020.

Richards, J. E., & Holley, F. B. (1999). Infants attention and the development of smooth pursuit tracking. *Developmental Psychology, 35*, 856–867.

Robinson, D. A. (1965). The mechanisms of human smooth pursuit eye movements. *Journal of Physiology, 180*, 569–591.

Rosander, K., & von Hofsten, C. (2000). Visual-vestibular interaction in early infancy. *Experimental Brain Research, 133*, 321–333.

Rosander, K., & von Hofsten, C. (2002). Development of gaze tracking of small and large objects. *Experimental Brain Research, 146*, 257–264.

Rosander, K., & von Hofsten, C. (2004). Infants' emerging ability to represent object motion. *Cognition, 91*, 1–22.

Rottach, K. G., Zivotofsky, A. Z., Das, V. E., Averbuch-Heller, L., Discenna, A. O., Poonyathalang, A., et al. (1997). Comparison of horizontal, vertical and diagonal smooth pursuit eye movements in normal human subjects. *Vision Research, 36*, 189–2195.

Sekuler, A. B., & Sekuler, R. (1993). Representational development of direction in motion perception: A fragile process. *Perception, 22*, 899–915.

Takeichi, N., Fukushima, J., Kurkin, S., Yamanobe, T., Shinmei, Y., & Fukushima, K. (2003). Directional asymmetry in smooth ocular tracking in the presence of visual background in young and adult primates. *Experimental Brain Research, 149*, 380–390.

von Hofsten, C., Feng, Q., & Spelke, E. S. (2000). Object representation and predictive action in infancy. *Developmental Science, 3*(2), 193–205.

von Hofsten, C., & Rosander, K. (1996). The development of gaze control and predictive tracking in young infants. *Vision Research, 36*, 81–96.

von Hofsten, C., & Rosander, K. (1997). Development of smooth pursuit tracking in young infants. *Vision Research, 37*, 1799–1810.

von Hofsten, C., Vishton, P., Spelke, E. S., Feng, Q., & Rosander, K. (1998). Predictive action in infancy: Tracking and reaching for moving objects. *Cognition, 67*, 255–285.