



Children's pursuit eye movements: a developmental study

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Abstract

We examined the pursuit eye movements of adults and three groups of children 4–6, 8–10, 12–16 years of age. The first experiment compared tracking performance of a partially occluded target with that of a fully visible target. The second experiment examined pursuit abilities of children using a non-cognitive source of information for motion, i.e., proprioception. In this experiment, we compared the ability to track one's own strobe-illuminated finger with the tracking of the experimenter's finger. In the first experiment, only children 4–6 years of age had difficulty inhibiting the tendency to look towards the visible portion of the partially occluded target. They also had significantly fewer epochs of pursuit relative to teenagers and adults. The older children's pursuit eye movements (8–10) were neither significantly different from the youngest nor from the two older groups. In the second experiment, all participants pursued their own finger better than the experimenter's finger, but the youngest children had significantly fewer epochs of pursuit relative to adults. Pursuit of a partially occluded target and incorporation of proprioceptive signals to drive smooth pursuit eye movements are abilities present at four years of age that continue to develop with increasing age.

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1. Introduction

In everyday life, objects are often partially concealed by other structures and we are required to mentally complete them and in some cases follow their movements. Human adults have the ability to smoothly pursue imaginary or partially occluded moving objects as effectively as actual moving targets at or near the fovea (Barnes, Goodbody, & Collins, 1995; Barnes & Hill, 1984; Glenny & Heywood, 1979; Steinbach, 1976; Wyatt, Pola, Fortune, & Posner, 1994). Children as young as 16 weeks of age are able to smoothly pursue a visible target (Lengyel, Weinacht, Charlier, & Gottlob, 1998). By 4 months of age, infants perceive partially occluded targets as uniform objects behind an occluder (Johnson, 2001; Johnson, Bremner, Slater, & Mason, 2000). However, whether children can smoothly pursue partially occluded targets has never been studied.

A number of studies have demonstrated that higher order abilities that may be an integral aspect of smooth pursuit eye movements, such as sustained visuospatial attention, incorporation of feedback information into pursuit movements, or mental tracking ability, appear to have a protracted developmental trajectory and seem to emerge around 8 years of age (Dean, Duhe, & Green, 1983; Haishi & Kokubun, 1995; Lengyel et al., 1998; Ross, Radant, & Hommer, 1994).

The present study explored children's ability to pursue a partially occluded target, referred to as the Cognitive Contour, hypothesizing that the cognitive abilities required to successfully pursue this target would emerge around 8 years of age. We also tested pursuit using a non-cognitive source of information for motion, proprioception. Steinbach (1969, 1976) has shown that proprioception provides an adequate stimulus for adult observers to pursue their own strobe-illuminated finger. We hypothesized that this ability would also be present in all the children we tested, regardless of age given that proprioceptive awareness of the body appears to be developed at a very early age (Rochat, Goubet, & Senders, 1999).

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2. Method

2.1. Subjects

Forty participants were recruited from advertisements. They were separated into four age-groups each consisting of 10 participants. The four age-groups included: children 4–6 years old, children 8–10 years old, adolescents 12–16 years old, and adults (20–36). Participants were paid a \$20 honorarium. All participants, by self-report (or by parents), were without neurological, vestibular, and oculomotor anomalies. Informed consent was obtained from participants 16 years of age and older, and from the parents of participants under 16 years of age. Assent was obtained from participants under 16.

2.2. Apparatus

Both horizontal and vertical eye movements were recorded using a video-based cornea/pupil tracking system (El-Mar Series 2020 Eye Tracker, Toronto, Canada). This system is free from drift and has a maximum resolution of 6 min of arc. It has a linear range of more than $\pm 25^\circ$ on the vertical meridian and above $\pm 30^\circ$ on the horizontal meridian. Eye movements were sampled at 120 Hz. The stimulus movement was recorded using a “Flock of Birds” magnetic tracker system. A sensor was affixed to a wrist band which went around the wrist of either the experimenter or the participant, depending on the condition, and it provided a record of the movement of the finger in the Strobe ex-

periment (described below), and the stimulus in the Cognitive Contour. This tracker system detected translational movements in three dimensions, accurate to 0.1 in. (2.54 mm). For each participant, the eye tracker was calibrated by recording eye positions at seven horizontal and vertical fixation points across a range of $\pm 10^\circ$ (visual angle). The head was stabilized by a chin-rest and a forehead rest. For each individual, the chin-rest height was adjusted such that the subject was looking straight ahead when looking at the 0° calibration target.

2.3. Procedure

2.3.1. Experiment 1, Cognitive Contour

Seated participants viewed the experimental stimulus from 57 cm away. Similar to that shown in Fig. 1 in Steinbach (1976), the pursuit stimulus was the bottom apex of an inverted isosceles triangle with a base of 25° and sides of 22° . The inverted triangle was moved irregularly (with varied frequency and amplitude) along a horizontal track across a range of 3° – 25° of visual angle by the experimenter. The Cognitive Contour experiment consisted of two conditions: in the visible condition (VIS), participants were required to track the visible corner of the triangle, and in the occluded condition (OCC), the triangle was partially occluded so that the bottom 8.4° of the triangle was covered and only parts of the upper edges were visible. The duration of each condition was 40 s.

In the OCC condition participants were asked to pursue the invisible corner, as if they could see it. If participants precisely followed these instructions, their

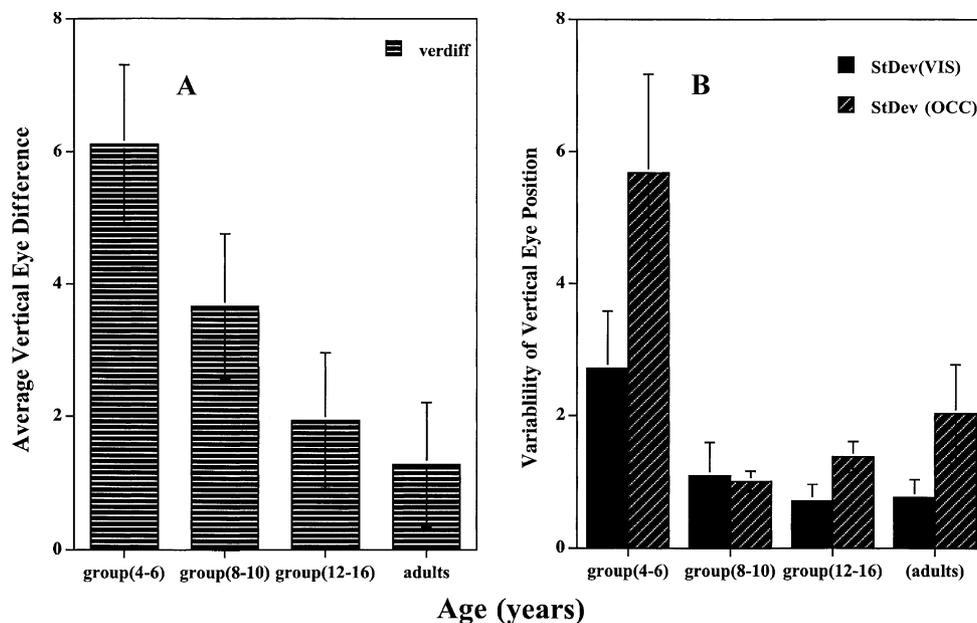


Fig. 1. (A) The average vertical eye difference between the VIS and OCC condition for all groups. (B) The variability of vertical eye positions of the participants in the OCC and VIS conditions of the Cognitive Contour. Note the greater variability for children 4–6 years of age in the OCC condition relative to the VIS condition.

vertical eye positions in the two conditions should have been alike. Eye movement data were collected under normal room illumination.

2.3.2. Experiment 2, Strobe

The second experiment tested participants' pursuit abilities under 5 Hz stroboscopic illumination (micro-second flash presented every 200 ms) using General Radio Model #1531 Strobotac. This experiment consisted of two conditions: (1) participants had to track the movement of their own strobe-illuminated finger (OWN), and (2) they were requested to pursue the experimenter's strobe-illuminated finger (EXP). Either the experimenter or the participant, depending on the particular condition, wore the wristband with the stimulus tracker attached to it. The finger movements were restricted by stops to a maximum of 27° (visual angle). The stops were fixed on a table in the frontal-parallel plane 40 cm from the participants' eyes.

In the OWN condition, participants were instructed to move their finger back and forth irregularly (as demonstrated by the experimenter) between the stops and then, to the best of their ability, smoothly pursue it. In the EXP condition, they were informed that the experimenter was going to move her finger back and forth irregularly and they were to try their best to follow the experimenter's finger. The duration of each condition was 40 s. The Strobe experiment was conducted immediately after the Cognitive Contour experiment. The two conditions in each experiment were presented in an alternating order between participants. The frequency of OCC and VIS conditions presented as the first condition was approximately equal within age groups, with the exception of the youngest children receiving the VIS condition more frequently as the first condition by chance (as a result of alternation between participants).

2.4. Data analysis

Since the saccadic system steps in and aids the pursuit system whenever retinal error accumulates, the frequency of saccades provides one measure of the ability of tracking efficacy (Abel & Ziegler, 1988). Hence, the data were first examined for frequency of saccades. Eye movements with peak velocities exceeding $50^\circ/\text{s}$ were identified as saccades by a custom-designed software program, AnYZII 3.3. The experimenter also visually reviewed the marked saccades to ensure that they were genuine and not blink artifacts. The number of saccades was determined over the entire 40 s session for each condition. In addition to saccade frequency, saccade amplitude was also computed and averaged. Following this analysis, the saccades were removed and the remaining segments constituted true smooth pursuit eye movements (Abel & Ziegler, 1988; Ross, Radant, & Hommer, 1993; Ross et al., 1994). These segments were

then differentiated to produce velocity data and the absolute values were exported to Microsoft Excel and averaged. This value constituted the average pursuit eye movement velocity of a participant in a given condition. The ratio of this average eye velocity to average target velocity in the same condition produced the velocity gain of the true smooth pursuit eye movements in that particular condition. The same procedure was used to analyze the data in both experiments.

In the Cognitive Contour experiment, participants' vertical eye movements were averaged for each of the two conditions. Then, these values were subtracted from each other for each group to examine the extent of discrepancy between the vertical eye positions in the two conditions. If participants were directing their gaze at the occluded apex position, then their average vertical eye positions in the OCC and the VIS conditions should be similar, and a discrepancy value close to zero should be obtained. The bottom apex of the inverted triangle, the target, was 8.4° below the visible horizontal edge of the occluder. If participants in the OCC condition were tracking one of the visible edges of the triangle, instead of the apex, then a difference of at least 8.4° in vertical eye position should be observed between the VIS and OCC condition.

3. Results

3.1. Experiment 1, Cognitive Contour

The first analysis done on the vertical eye position data of the participants was to determine whether they were following instructions and pointing their gaze below the visible contours and staying close to the position of the occluded apex. A univariate analysis of variance (ANOVA) for the difference between the average vertical eye positions in the OCC and the VIS conditions reached a trend, but not significance, $F(3, 36) = 2.59$, $p < 0.068$. A closer look at the vertical difference values revealed three odd values. These three extreme values were: 17.2 (a participant in the youngest group), 21.2 (a participant in the 8–10 year olds group), and 13.1 (a participant in the adults group) degrees of visual angle. These values indicate that the participants were looking, on average, at points above the stimulus apparatus. A test of studentized residuals and Cook's distance (Tabachnick & Fidell, 2000) identified these three points as outliers that greatly influence and distort the data. The data associated with these three individuals were deleted completely for the rest of the statistical analysis. A separate univariate ANOVA without these three extreme values revealed a significant difference between the age groups, $F(3, 34) = 5.047$, $p < 0.005$ (Fig. 1A). Further analysis using Tukey HSD showed a significant difference in this variable between the youngest children

Table 1

Vertical eye discrepancy and distance from visible contours both with (a) and without (b) the extreme values

| (a) Extreme values included | | | (b) Extreme values excluded | |
|-----------------------------|---------------------|-------------------------------------|-----------------------------|-------------------------------------|
| Age groups | Vertical difference | Distance away from visible contours | Vertical difference | Distance away from visible contours |
| 4–6 | 7.22 | 1.18 | 6.11 | 2.29 |
| 8–10 | 5.41 | 2.99 | 3.66 | 4.74 |
| 12–16 | 1.94 | 6.46 | 1.94 | 6.46 |
| adults | 2.46 | 5.94 | 1.28 | 7.12 |

(4–6 years) and the teenagers, $p < 0.04$; and a significant difference between the youngest children and the adults, $p < 0.02$.

Exploring the difference in vertical eye position between the two conditions for each group reveals that the nearest moving edge was, on average, approximately 2° off the fovea for the youngest group, about 4.7° off the fovea for the 8–10 year olds, about 6.4° for the teenagers, and in adults the nearest moving edge was about 7° off the fovea (see Table 1). These data coupled with the statistical data indicate that only the youngest children were unable to maintain their gaze close to the location of the occluded target. In order to examine whether the youngest children were consistently close to the visible edges or had episodes of eccentric pursuit that they could not sustain continuously, standard deviations of the vertical eye position of each participant in each condition of the Cognitive Contour was analyzed. Small standard deviations reflect greater consistency and less variability in the vertical eye position of the individual in a given condition (VIS or OCC). As the standard deviation increases, it indicates alternating between eccentric pursuit and pursuit closer to the visible edges.

A repeated measures analysis of variance revealed a main effect for condition, $F(1, 33) = 9.585$, $p < 0.004$, a between groups effect for age, $F(3, 33) = 7.02$, $p < 0.001$ and a trend for interaction effect, $F(3, 33) = 2.765$, $p < 0.057$ (see Fig. 1B) in the vertical eye position variability. Further exploration of the data using Tukey HSD post hoc test showed a significant difference between the youngest children (4–6 years) and the older children (8–10 years), $p < 0.003$, between the youngest children and the teenagers, $p < 0.002$, and the youngest children and the adults, $p < 0.009$. This indicates that the youngest children had difficulty maintaining their gaze at the occluded apex and had to look up towards the visible contours periodically. The same difficulty was not observed in the other three groups.

The next series of analyses was carried out on the horizontal eye movement data. The pursuit eye movements of a 6-year-old participant in the VIS and the OCC conditions can be seen in Fig. 2. There are clear epochs of smooth pursuit in both conditions, but the OCC condition yielded larger saccades, and a reduced amount of pursuit.

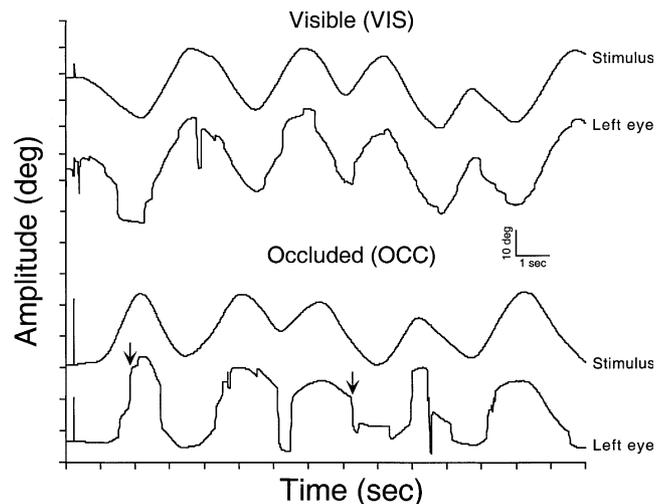


Fig. 2. The pursuit eye movements (saccades included) of a 6 year old participant along with the stimulus trace in the VIS and OCC conditions of the Cognitive Contour. Note the increase in saccade amplitude in the Occluded Apex condition (the arrows mark two of the saccades).

A repeated measures analysis of variance revealed a significant main effect for pursuit gain between the OCC and VIS conditions, $F(1, 33) = 110.878$, $p < 0.001$, and a between groups effect for age, $F(3, 33) = 5.843$, $p < 0.003$. Further exploration of the data using Tukey HSD post hoc test revealed a significant difference in pursuit gain between the youngest children and the teenagers ($p < 0.01$), and the youngest children and the adults ($p < 0.003$). Fig. 3A shows the average pursuit gains (saccades removed) of the four age groups in both the OCC and the VIS conditions. All age groups performed similarly when they followed the visible target. However, a significant difference in performance becomes evident in the OCC condition of the Cognitive Contour between the age groups.

Similar results were obtained for saccade amplitude. A repeated measures analysis of variance revealed a main effect for condition (see Fig. 3B), $F(1, 33) = 97.748$, $p < 0.001$, a between groups effect for age, $F(3, 33) = 6.183$, $p < 0.002$, and an interaction between age and condition $F(3, 33) = 4.27$, $p < 0.01$. All participants had significantly larger saccades in the occluded condition. A Tukey HSD test revealed significant differences in saccadic amplitude between the youngest children and

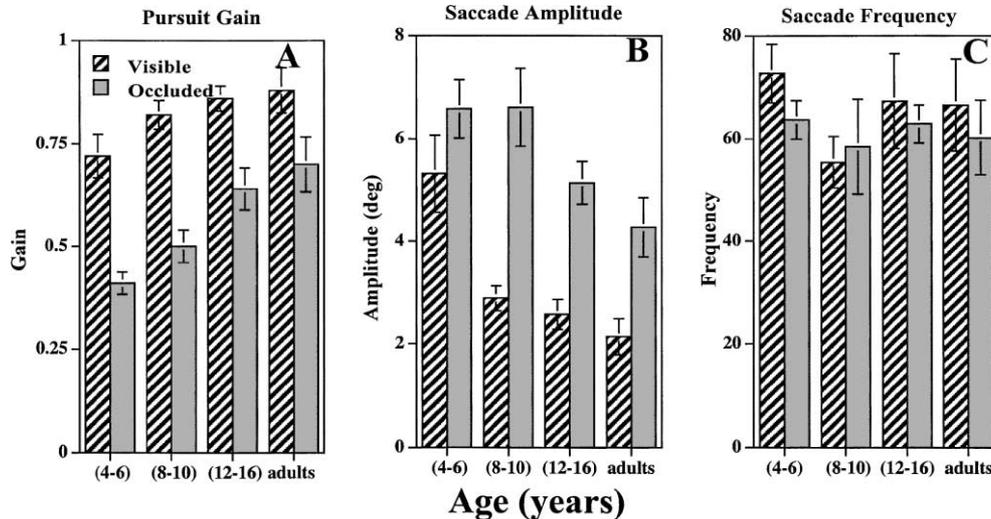


Fig. 3. (A) Pursuit gain of the four groups in the VIS and OCC conditions of the Cognitive Contour. (B) Average saccade amplitude for each group in the two conditions of the Cognitive Contour. (C) Averaged total saccade frequency for a 40 s experimental session for the four groups in the two conditions of the Cognitive Contour.

the teenagers, $p < 0.017$; and the youngest children and the adults, $p < 0.002$.

The repeated measure analysis of variance did not reveal a significant difference in saccade frequency between the two conditions. Similarly no effects for age, and no interaction effects were found for this variable (see Fig. 3C).

3.2. Experiment 2, Strobe

Generally, participants were able to smoothly pursue their own finger with greater accuracy and more epochs of smooth pursuit than they were able to follow the experimenter's finger. Fig. 4 shows the pursuit eye movements of a 14-year-old participant in the EXP and the OWN conditions. Note that there are a greater number of saccades, larger saccades, and a reduced amount of pursuit in the EXP condition.

Repeated measures analysis of variance revealed a significant main effect for condition, $F(1, 33) = 26.347$, $p < 0.001$, and a between groups effect for age, $F(3, 33) = 3.464$, $p < 0.27$ (see Fig. 5A) in pursuit gain. There were no interaction effects. Post hoc tests revealed a significant difference between the youngest children's performance and those of the adults $p < 0.01$, there were no other significant differences between any other groups in the post hoc tests.

The analysis revealed a significant main effect for condition in saccade amplitude, $F(1, 36) = 16.68$, $p < 0.001$ (see Fig. 5B). There were no interaction effects, and no effects for age in saccade amplitude. There was a significant effect for condition in saccade frequency $F(1, 33) = 17.739$, $p < 0.001$, but no significant interactions and no effects for age in this variable. Fig.

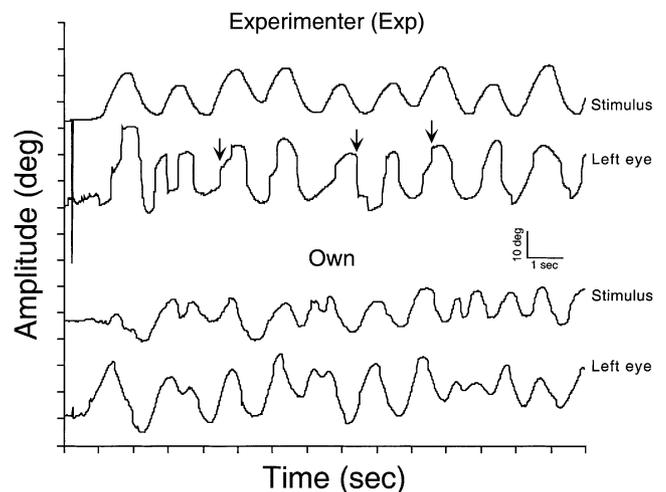


Fig. 4. The stimulus and eye movement traces of a 14 year old participant in the EXP and OWN conditions of the Strobe experiment. The eye movement and stimulus traces were separated for clarity. Note the greater number of saccades in the EXP condition (arrows mark three of the saccades).

5C shows the average saccade frequency of each group in both the EXP and OWN conditions.

4. Discussion

4.1. Cognitive Contour

Although pursuit eye movements were made, observers had more difficulty smoothly pursuing the occluded apex. The youngest children's pursuit gain was significantly decreased relative to the teenagers' and

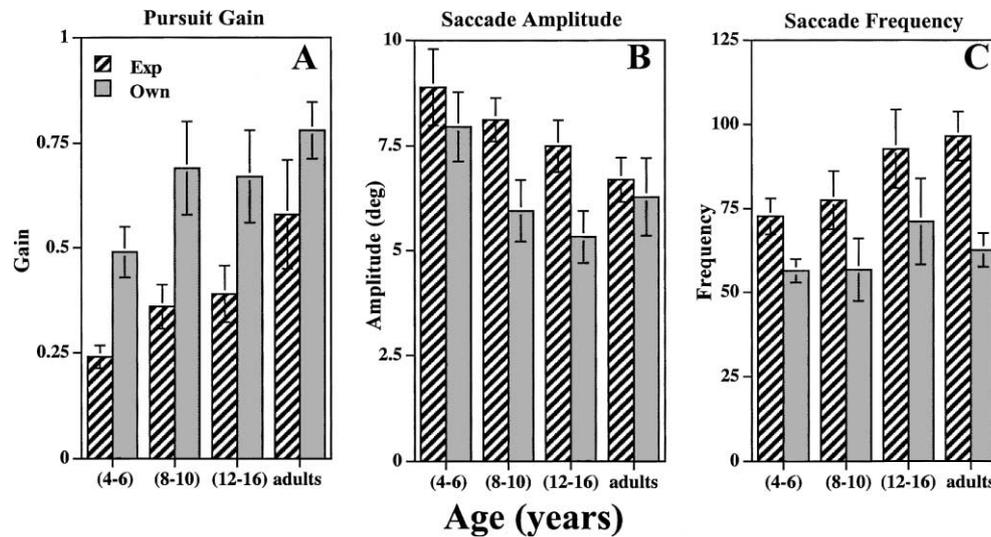


Fig. 5. (A) Average pursuit gain for the four groups in the OWN and EXP conditions of the Strobe experiment. (B) Average saccade amplitude for each group in both conditions of the Strobe experiment. (C) Averaged total saccade frequency for each group in both conditions of the Strobe experiment.

adults' pursuit gains in this condition. Since the interaction did not reach significance, this pursuit difficulty can not be attributed to the OCC condition alone. However, Fig. 2A. does depict participants' greater difficulty with the OCC condition relative to the VIS condition, with the two youngest groups displaying the least smooth pursuit in this condition. This figure also shows a regular increase in pursuit gain in the OCC condition between the age groups, with gain being the lowest in the youngest children and the highest in the adults. This is indicative of an age trend, rather than an abrupt improvement in children's pursuit ability who are 8 years and older contrary to our initial hypothesis. The developmental trajectory of this ability appears to be protracted, gradual, and continues to develop beyond age 8.

Similar to pursuit gain, the results revealed that all groups had higher saccadic amplitudes in the occluded condition relative to the visible condition. This finding is consistent with the existing literature, which maintains that as smooth pursuit gain decreases saccadic frequency and/or amplitude increases (Engelken, Stevens, & Bell, 1994; Lisberger, Morris, & Tychsen, 1987). Figs. 2A and B illustrate pursuit gains and saccadic amplitudes of all age groups and their complementary relationships. As depicted in these figures, an increase in saccadic amplitude compensates for the reduction in gain.

The results revealed differences between average vertical eye position of the participants in the VIS and in the OCC conditions. These differences, however, were less than the vertical distance of the nearest visible edge to the target, indicating that all participants were following the instructions and directing their gaze below the visible moving contours. Fig. 1A (average vertical eye difference) illustrates a progressive decrease in the

average vertical eye difference between the age groups, with the youngest age group having the greatest vertical discrepancy and adults having the least. The statistical analyses revealed a significant difference in this variable between the youngest group and teenagers, and the youngest group and adults. This suggests that teenagers and adults performed very similarly, but significantly different from 4 to 6 year olds. The 8–10 year olds neither performed significantly different from the youngest group nor significantly different from the two older groups.

Alternatively, Fig. 1B clearly depicts a difference in vertical eye position variability between the youngest children and all the other groups. The statistical analyses also demonstrated significant differences in vertical eye position variability between the youngest children and older children, youngest children and teenagers, and youngest children and adults. This contrasts with the results of vertical eye position difference, in which the 8–10 year olds did not differ significantly in their performance from the youngest group, or any of the two older groups. This suggests that all integrated features of the ability to pursue partially occluded targets do not mature at the same rate. The older children (8–10) did not exhibit difficulty inhibiting the tendency to look up at the visible contours as indicated by the low standard deviation in the vertical eye position variability. However, with pursuit gain and vertical eye position difference they performed mid-way between the two older groups and the youngest group.

It is difficult to identify the underlying systems that may be responsible for the difficulty displayed by the two youngest groups, especially children 4–6 years of age, in pursuing a partially occluded target. Several imaging studies have demonstrated that the frontal eye

field (FEF), the supplementary eye field (SEF), the precuneus, the parietal eye field (PEF), the medial temporal (MT) and superior medial temporal (MST), and the anterior and posterior cingulate cortexes subserved the visually guided smooth pursuit eye movements (Berman et al., 1999; O'Driscoll et al., 1998; Petit & Haxby, 1999). Two of these cited regions; namely the FEF and the SEF are located within the frontal cortex. It is possible that a slightly different neural circuitry underlies tracking of a more cognitive target such as the partially occluded target, perhaps involving a greater spatial extent of the frontal regions already implicated in the visually guided pursuit eye movements. The pursuit difficulty that the two youngest groups displayed may be stemming from any systems located within combinations of these areas.

The vertical eye movement data appear to implicate the frontal cortex as one of the regions underlying at least part of the difficulties exhibited by the youngest children in pursuing a partially occluded target. The analysis of the variability of their vertical eye position showed that their eyes were shifting position, moving up towards the visible contours and then moving back down close to the occluded apex. This indicates that they were trying to look at the occluded apex, but had difficulty inhibiting the tendency to look up at the visible edges. Inhibitory controls have been suggested to be a function of the frontal cortex (Roberts, Hager, & Heron, 1994; Roberts & Pennington, 1996). It is likely that this difficulty, exhibited only by the youngest children, is associated with the frontal cortex.

An alternative hypothesis stems from the work of Stone and Beutter (2000). These investigators manipulated the perceived motion of partially occluded targets to determine if human pursuit is driven exclusively by the image motion on the retina or if it is related to perceived object motion. Their findings suggest that the pursuit system utilizes converging signals from attentional, perceptual, and cognitive inputs to drive smooth pursuit eye movements. The investigators suggest that the integration of local motion signals likely begins in the middle temporal (MT) area and in the medial superior temporal (MST). Accordingly, both of these areas appear to be particularly critical in the generation of perceived object motion. Although these four areas (MT, MST, FEF and SEF) are possible regions underlying the pursuit difficulties that our two youngest groups displayed, further research is required to substantiate and verify the primary systems responsible for the pursuit difficulties exhibited by our two youngest groups.

4.2. Strobe

Pursuit gain was significantly lower when participants followed the experimenter's finger compared to when

they tracked their own finger, consistent with Steinbach's (1969) findings and hypothesis that proprioception from the arm provides information for pursuit. Under stroboscopic illumination, there are intermittent periods of darkness and light. During the dark intervals, when one is required to track his/her own finger, the only sources of information on the movement of the target are the efferent signals sent to move the limbs and the afferent signals coming back from the muscle and joint receptors. Steinbach (1969) showed that the proprioceptive signals (the afferent signals) were mainly responsible for the ability to pursue one's own finger under stroboscopic illumination. When an individual is tracking the experimenter's finger, during the dark intervals, in addition to a lack of continuous visual feedback, the proprioceptive information is also not available. Therefore, it should be impossible to smoothly pursue the experimenter's finger. We found, however, some smooth pursuit of the experimenter's finger and this may be because the 5 Hz (200 ms interval) stroboscopic illumination was just at the threshold of apparent movement [optimal ϕ movement is perceived when stimuli are flashed at interval rates of 60–200 ms (Graham, 1966)]. As expected, reduction in pursuit gain was compensated for by a significant increase in both saccade amplitude and saccade frequency in the EXP condition for all participants.

In the strobe experiment, pursuit gain, saccade amplitude and saccade frequency revealed no interaction effects, but analysis did show an age effect in pursuit gain only. Post hoc tests revealed a significant difference between the performances of the youngest children and those of adults. This finding appears to indicate that incorporating proprioceptive signals to drive smooth pursuit eye movements continues to develop beyond age 6. This is not consistent with our hypothesis that all age groups should perform similarly in this experiment. Visual inspection of Fig. 5A depicts a progressive improvement of pursuit gain from the youngest to the oldest group.

5. Conclusion

Pursuit of a partially occluded target and incorporation of proprioceptive signals to drive smooth pursuit eye movements both appear to continue to develop beyond 8 years of age. However, statistical analysis does point out to significant differences between the performances of children 4–6 years of age and teenagers, and children 4–6 and adults, and in the variability of vertical eye position, between the youngest group and all the other groups. These findings are suggestive of a developmental trajectory that is steepest between the age of 6–12. It is our speculation that the pursuit difficulties exhibited by the children in this age range may be

related to the structural immaturity of the frontal cortex or its still proliferating cortical pathway projections.

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References

- Abel, L. A., & Ziegler, A. S. (1988). Smooth pursuit eye movements in schizophrenics: What constitutes quantitative assessment? *Biological Psychiatry*, *24*, 747–761.
- Barnes, G., Goodbody, S., & Collins, S. (1995). Volitional control of anticipatory ocular pursuit responses under stabilized image conditions in humans. *Experimental Brain Research*, *106*, 301–317.
- Barnes, G. R., & Hill, T. (1984). The influence of display characteristics on active pursuit and passively induced eye movements. *Experimental Brain Research*, *56*, 438–447.
- Berman, R. A., Colby, C. L., Genovese, C. R., Voyvodic, J. T., Luna, B., Thulborn, K. R., & Sweeney, J. S. (1999). Cortical networks subserving pursuit and saccadic eye movements in humans: an fMRI study. *Human Brain Mapping*, *8*, 209–225.
- Dean, A. L., Duhe, D. A., & Green, D. A. (1983). The development of children's mental tracking strategies on a rotation task. *Journal of Experimental Child Psychology*, *36*, 226–240.
- Engelken, E. J., Stevens, K. W., & Bell, A. F. (1994). The application of smooth pursuit eye movement analysis to clinical medicine. *Aviation, Space, and Environmental Medicine*, *65*, A62–65.
- Glenny, G., & Heywood, S. (1979). Hans Gertz revisited: the different effects of invisibility and darkness on pursuit eye movements. *Perception*, *8*, 31–36.
- Graham, C. H. (1966). Perception of movement. In C. H. Graham, N. R. Bartlett, J. L. Brown, Y. Hsia, C. G. Mueller, & L. A. Riggs (Eds.), *Vision and visual perception* (pp. 575–588). New York: John Wiley and Sons Inc.
- Haishi, K., & Kokubun, M. (1995). Developmental trends in pursuit eye movements among preschool children. *Perceptual and Motor Skills*, *81*, 1131–1137.
- Johnson, S. P. (2001). Visual development in human infants: binding features, surfaces, and objects. *Visual Cognition*, *8*(3/4/5), 565–578.
- Johnson, S. P., Bremner, J. G., Slater, A. M., & Mason, U. C. (2000). The role of good form in young infants' perception of partly occluded objects. *Journal of Experimental Child Psychology*, *76*, 1–25.
- Lengyel, D., Weinacht, S., Charlier, J., & Gottlob, I. (1998). The development of visual pursuit during the first months of life. *Graefé's Archives of Clinical Experimental Ophthalmology*, *236*, 440–444.
- Lisberger, S. G., Morris, E. J., & Tychsen, L. (1987). Visual motion processing and sensory-motor integration for smooth pursuit eye movements. *Annual Reviews of Neuroscience*, *10*, 97–129.
- O'Driscoll, G. A., Strakowski, S. M., Alpert, N. M., Matthyse, S. W., Rauch, S. L., Levy, D. L., & Holzman, P. S. (1998). Differences in cerebral activation during smooth pursuit and saccadic eye movements using positron emission tomography. *Biological Psychiatry*, *44*, 685–689.
- Petit, L., & Haxby, J. V. (1999). Functional anatomy of pursuit eye movements in humans as revealed by fMRI. *The Journal of Neurophysiology*, *82*(1), 463–471.
- Roberts, R. J., Jr., Hager, L. D., & Heron, C. (1994). Prefrontal cognitive processes: working memory and inhibition in the antisaccade task. *Journal of Experimental Psychology: General*, *123*, 374–393.
- Roberts, R. J., & Pennington, B. F. (1996). An interactive framework for examining prefrontal cognitive processes. *Developmental Neuropsychology*, *12*(1), 105–126.
- Rochat, P., Goubet, N., & Senders, S. J. (1999). To reach or not to reach. Perception of body effectivities by young infants. *Infant and Child Development*, *8*(3), 129–148.
- Ross, R. G., Radant, A. D., & Hommer, D. W. (1993). A developmental study of smooth pursuit eye movements in normal children from 7 to 15 years of age. *Journal of the American Academy Child and Adolescent Psychiatry*, *32*, 783–791.
- Ross, R. G., Radant, A. D., & Hommer, D. W. (1994). Open- and closed-loop smooth-pursuit eye movements in normal children: An analysis of a step-ramp task. *Developmental Neuropsychology*, *10*(3), 255–264.
- Steinbach, M. J. (1969). Eye tracking of self-moved targets: the role of efference. *Journal of Experimental Psychology*, *82*(2), 366–376.
- Steinbach, M. J. (1976). Pursuing the perceptual rather than the retinal stimulus. *Vision Research*, *16*, 1371–1376.
- Stone, L. S., & Beutter, B. R. (2000). Visual motion integration for perception and pursuit. *Perception*, *29*, 771–787.
- Tabachnick, B. G., & Fidell, L. S. (2000). *Using multivariate statistics*. New York: Allyn & Bacon.
- Wyatt, H. J., Pola, J., Fortune, B., & Posner, M. (1994). Smooth pursuit eye movements with imaginary targets defined by extrafoveal cues. *Vision Research*, *34*, 803–820.