Integrated global motion influences smooth pursuit in infants

Olga Kochukhova
Department of Psychology, Uppsala University, Uppsala, Sweden

Kerstin Rosander
Department of Psychology, Uppsala University, Uppsala, Sweden

Smooth pursuit eye movements (SP) were studied in 5- and 9-month-old infants and adults in response to a rhombus oscillating horizontally behind three spatially separated vertical occluders. During motion, the rhombus vertices were never visible. Thus the perception of the global motion of the rhombus required integration of its moving visible segments. We tested whether infants were able to use such perceived global motion for SP in two different occluder conditions; one in which the occluder was clearly visible to the observer and one in which it was invisible. In adults, the presence of a visible occluder hiding the vertices of the rhombus strongly facilitates the perception of the global motion. It was found that adults and 9-month-olds performed significantly more horizontal SP in the presence of a visible occluder but not 5-month-olds. Furthermore, this tendency was strengthened over single trials, and this temporal pattern was very similar in all age groups. In the invisible occluder condition both adults and infants tracked the segments of the rhombus primarily with vertical SP. It was concluded that the ability to integrate moving object fragments into perceived global motion and use that to regulate SP develops into adult performance by 9 months of age.

Keywords: infants, smooth pursuit, global motion, perception

Citation: Kochukhova, O., & Rosander, K. (2008). Integrated global motion influences smooth pursuit in infants. *Journal of Vision, 8*(11):16, 1–12, http://journalofvision.org/8/11/16/, doi:10.1167/8.11.16.

Introduction

Objects moving in a cluttered environment are frequently occluded from view by other more nearby objects. Only fractions of an observed object may be simultaneously visible. In such situations, the perception of a moving integrated object relies on the ability to unite those fractions. This ability constitutes one of the most basic principles of perception; the gestalt law of common motion (Johansson, 1950). The component motions making up the global motion do not necessarily move in the same direction. Even when the components move orthogonally, they combine into a common motion of the whole group and the residual motions are perceived as relative motions within the group.

The sensitivity to global motion coherence develops very early in life. This has been demonstrated in three different ways. The first evidence comes from the habituation paradigm. Kellman and Spelke (1983) showed that 4-month-old infants, who were habituated to a display consisting of a rod moving back and forth behind an occluder, dishabituated to the visible parts moving without the occluder but not to a moving complete rod. A number of replications of this demonstration have been carried out in different contexts and in different age groups (Johnson & Aslin, 1995, 1996; Johnson & Nañez, 1995; Kellman, Gleitman, & Spelke, 1987; Kellman, Spelke, & Short, 1986; Slater et al., 1990). All these studies demonstrate that coherently moving parts sticking out from behind an occluder are perceived by infants as belonging to the same object. Recently, Johnson, Slemmer, and Amso (2004) studied the scanning patterns of 3-month-old infants while they habituated to this type of stimuli. It was found that those infants, whose post-habituation preferences could be interpreted as unity perception, scanned more frequently around the rod and across the range of its motion. Thus, the infants scanned systematically in a way that optimized the intake of the important information for unity perception.

The second kind of evidence of the development of global motion perception comes from visual evoked potentials (Braddick et al., 2005; Wattam-Bell, Birtles, Braddick, & Atkinson, 2005). The results of these studies suggest that both global and local motion processing and local form processing precede development of global form processing. On the basis of these results Braddick et al. (2005) suggested that extra-striate global mechanisms for motion become functional soon after cortical directional selectivity has developed.

The third evidence of early expressions of global motion perception comes from the study of directional eye movements (Kowler & McKee, 1987). In this method an observer, unaware of the direction of stimulus motion, views the infant's eye movements and/or optokinetic nystagmus (OKN) and takes decision on the direction of

doi: 10.1167/8.11.16 Received March 16, 2007; published August 22, 2008 ISSN 1534-7362 © ARVO

the gaze movements. The assumption is that the infants will move their eyes in the direction of the perceived motion. Using this measurement, Manny and Fern (1990) found that 1- to 3-month-old infants show eye movements in the direction of coherent motion when seeing a single grating or a plaid composed of two perpendicular gratings through a round aperture. Dobkins, Fine, Hsueh, and Vitten (2004) made the task more complicated. They presented 2- to 5-month-old infants with a field of moving grating apertures. Each of them contained one of two motion directions, and they were placed across the screen in a counterbalanced order. Dobkins et al. (2004) showed that all infants could integrate component motions into coherent global pattern motion and this integration occurred over rather large regions of space.

The purpose of the present study was to investigate the evolving relationship between perceived global motion and smooth pursuit eye movements (SP) in development. Although the results of Dobkins et al. (2004) show that infants' eye movements are related to the global motion of a composite motion display, they did not investigate whether those eye movements are smooth or saccadic. This is an important question because it informs about how SP is controlled. One possibility is that SP is controlled by single motion elements on the retina, i.e. "retinal slip" (Leigh & Zee, 1999; Robinson, 1965). The alternative is that SP is controlled by the integrated global motion of displayed motion elements. Another way to formulate this question is to ask whether SP is controlled by internal or external coordinates.

Perceiving the coherent motion of a composite motion pattern is a necessary but not a sufficient condition for stabilizing gaze on it with smooth pursuit. Earlier research indicates that infants perceive the global motion of a group of motion components from at least 2 months of age (Dobkins et al., 2004). Smooth pursuit of horizontal linear motion reaches an adult-like level around 4 months of age (Rosander & von Hofsten, 2000, 2002; von Hofsten & Rosander, 1997). Thus, from that age, the degree by which infants use perceived object motion to regulate smooth pursuit of the motion should be a reliable indicator how well both parts of the system are integrated.

In the present study we compared the smooth pursuit response of 5- and 9-month-old infants and adults to a line-figure rhombus (see Figure 1 in the General methods section; stimulus adapted from Beutter and Stone, 2000) moving horizontally behind 3 stationary vertical occluders. Three sets of questions were asked. The first one had to do with the conditions under which infants perceive the global motion of the partly occluded line-figure rhombus. In adults, it relates to the contrast between the moving segments and the occluders. Beutter and Stone (2000), Lorenceau and Shiffrar (1992), and Stone, Beutter, and Lorenceau (2000) have shown that a simple change in the luminance of the occluders has dramatic effects on the perception of the moving segments. If the occluders are visible, adults perceive the global motion of a united object that continues behind the occluding parts, but if the occluders are of the same color as the background, adults only perceive the separate motions of the segments but not the coherent motion of a single object. Do infants perceive these patterns in the same way as adults? If infants perceive global motion in the case of the visible occluders then we should observe that the horizontal component of the SP will be generally larger with the visible occluders than with the invisible ones.

The second set of questions was related to the way the infants track a partly occluded line-figure stimulus. More specifically, do infants, who perceive the global motion of a partly occluded object, track it with smooth pursuit? In other words, the question is whether smooth pursuit is influenced by perceived motion of external objects or by the local displacements of stimulus elements on the retina. To be able to smoothly track the motion of a perceived object from the composite motions of its moving parts requires both perception of its global motion and ability to use this information to regulate smooth pursuit. Although the smooth pursuit of horizontal linear motion is adult-like from around 4 months of age, the neural processes underlying the control of smooth pursuit from perceived global motion of motion fragments may not be mature until much later. Therefore it becomes important to trace this developmental process. In the present study we evaluated infants' tendency to track global motion with smooth pursuit at both 5 and 9 months of age.

The third set of questions was related to how the SP response evolves during the viewing of a group of moving object parts. Is smooth pursuit of the global motion triggered as soon the composite moving stimulus is presented or does the perception of a moving whole become more salient with exposure time? If the latter alternative is valid, it is also possible that the perception of global object motion or the motion of its separate segments can switch back and forth with attentional fluctuations. On the other hand, if the smooth pursuit system becomes more entrained to the perception of global motion over the exposure time, this response will be more dominant toward the end of presentations than at the beginning.

General methods

Subjects

Altogether 41 infants in two different age groups were analyzed. Twenty infants (11 girls and 9 boys) were 38 ± 2 weeks old, and 9 girls and 12 boys were 22 ± 1 weeks old. All of them were healthy and born within 2 weeks of the expected date. Additional 9 infants were excluded from the experiment due to fussing and 4 due to bad reflection from the eyes. The third group consisted of

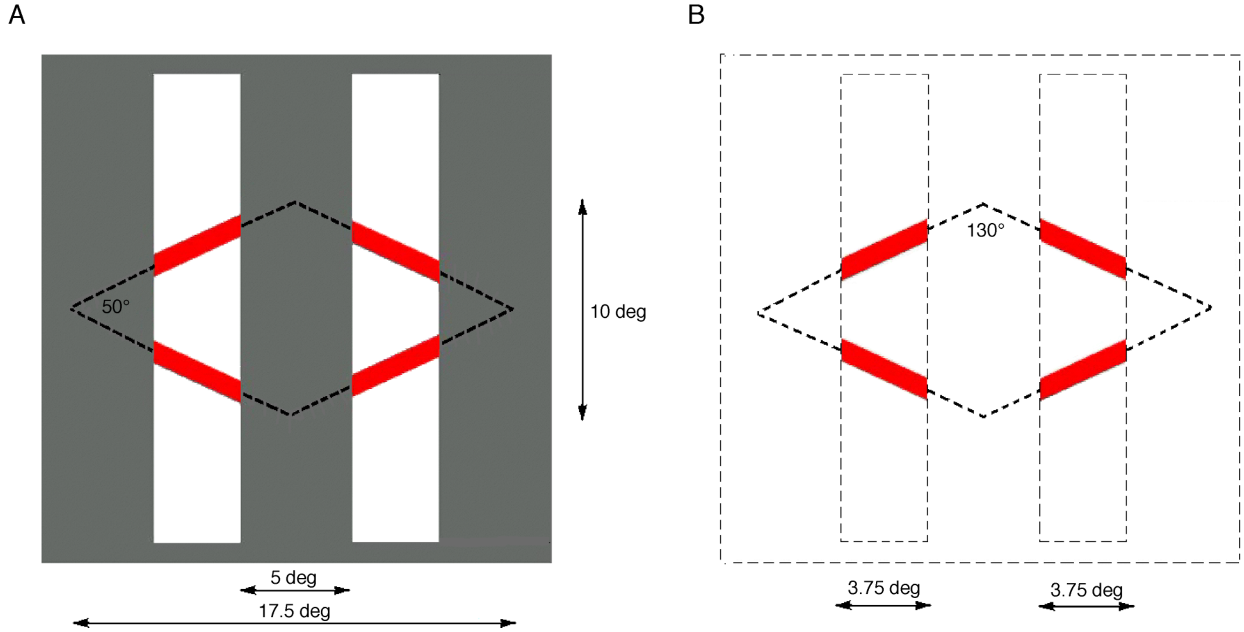

Figure 1. Stimuli used in the experiment. (A) Visible and (B) invisible occluder condition. The rhombus moved sinusoidally along a horizontal trajectory at a frequency of 0.33 Hz (peak velocity = 3.4°/s). The vertical amplitude of the visible segment motions was 1.5° and the horizontal amplitude of the rhombus motion was 2.5° of visual angle.

14 "naïve" adults (9 women and 5 men) in age range 23–54 years with mean age of 32.5 years.

Stimuli and apparatus

Gaze was measured with a Tobii 1750 eye tracker (17″ monitor) with an infant add-on (www.Tobii.se). At 60 cm viewing distance, the full display subtended 24° × 28°. The system records the reflection of near infrared light in the pupil and the cornea of both eyes at 50 Hz (accuracy = 0.5°, spatial resolution = 0.25°). During calibration, a blue and white sphere presented on the screen (provided by the courtesy of S. Johnson) expanded and contracted (extended diameter = 3.3°) in synchrony with a sound.

The experimental display is shown in Figure 1. It consisted of a white background (22.5° × 22.5°) on which a line-figure rhombus (height = 10°; width = 17.5°; line segments thickness = 0.6°) moved sinusoidally along a horizontal trajectory at a frequency of 0.33 Hz (peak velocity = 3.4°/s). Three vertical rectangles either of a white or a gray color covered the motion of the rhombus in such a way that its vertices were never visible (Figure 1). The covering rectangles were placed on an angular distance of 3.75° from each other. The width of each of them was 5°. The horizontal amplitude of the object motion was 2.5° and during one trial (24 s) it completed 8 full cycles of motion. The rhombus had vertex angles of 50° and 130° and was symmetrical about both the horizontal and vertical axes. Thus, during each trial the subject only saw the four line segments falling within the two apertures between the covering rectangles. The vertical amplitude of each segment motion was 1.5°. For each participant two different occluder conditions were presented: *visible* and *invisible*. In the *visible occluder* condition the white background rectangle was covered by three dark gray occluders in-between which the parts of moving rhombus were visible (Figure 1A). In the *invisible occluder* condition, the occluders and the background was of the same white color (Figure 1B). In both conditions the stimulus could start to move from the central position behind the middle occluder either to the left or to the right and to make the session less boring for infants, the moving rhombus could be either red or blue. In both conditions, the starting direction of the motion and the color of the rhombus were counterbalanced.

Experimental procedure

Families were contacted with a letter describing the study and an inviting to participate. If they decided to take part in the experiment, an appointment was made. Once in the laboratory each family was provided with a verbal description of the study, its purpose, and the methods used. The parents signed a consent form before the study began. The study was performed in accordance with the ethical standards specified in the 1964 Declaration of Helsinki and was approved by the ethics committee of Uppsala University.

The infant was seated in a safety car seat that was placed on the participating parent's lap 60 cm in front of the Tobii eye tracker and monitor. Before the experiment started, a calibration procedure was carried out. In preparation for the calibration, the experimenter adjusted the eye tracker to make sure that the reflections of both eyes were centered in the field of view of the cameras. During calibration a blue and white ball appeared on each of 9 calibration points at the screen in a random order. If the infants' attention was drawn to other parts of the visual field during this procedure the experimenter could present alternative movies with novel sounds at the current calibration location. At the end of the calibration, a graph appeared that reported how successful the calibration was; any unsuccessfully calibrated points were then recalibrated. In the experiment proper, subjects were presented with one session of 8 movies each containing 8 full cycles of the rhombus motion. In order to improve the infants' attention, movies were presented in combination with different kind of artificial sounds. In between movies, the infants were presented with one of 8 different attention grabbing movies (horizontal and vertical extension = 5.7°) displaying a small toy that moved and sounded in the middle of the screen. Each experimental session lasted no more than 6 minutes.

After the experiment the parent was shown the recorded gaze movements. As a compensation for their participation the parent received either gift certificate for a CD or for a toy shop (value 12 €).

The procedure for the adult group was similar to the infant group. The subject sat in front of the screen observing the movie. No information was given about the purpose of the experiment until it was finished. The reason was that we wanted to put the adults in the same conditions as the infants, to whom we could not give any instructions where to look on the screen. Thus, the adults did not know which pattern on the screen they should watch and follow. The instruction was "just watch the screen."

After the experiment the adult participants were asked what they were able to observe. No questioning was performed during the experiment to exclude the possibility that such a procedure would trigger a desire to attend to special parts of the moving object. Then it would be difficult to compare the results with those of the infant groups.

After completing the experiment, the adult participants received one movie ticket (value 10 €).

Data analysis

The gaze records were inspected to determine whether the subjects attended to the object. If a subject attended to the object motion less than 1/3 of the time during 1 experimental trial, this trial was excluded from the analysis. In order to be included in the analysis, participants had also to be attentive at least 1/3 of the trials. The tracking was analyzed in a spatial-temporal frame of reference with programs written in the Matlab (Mathworks Inc.) environment. The horizontal and vertical components of tracking were analyzed separately. The statistical analysis was performed in SPSS.

Tobii cornea reflection eye tracker (Tobii Technology AB) registers gaze. This means that eye movements and head movements cannot be separated. Head movements, however, are primarily involved in the tracking when the amplitude of the object motion is large. In the present study the horizontal amplitude of the stimulus motion was only 2.5° and should not elicit any head movements correlated with the smooth pursuit. To confirm this assumption, we checked the distances from each eye to the display screen for each subject over single trials. If the head turns, the relation between these distances will change. It was found that this was not the case and that the smooth gaze movements registered by the eye tracker were consequently smooth pursuit eye movements.

To calculate the smooth pursuit, eye movement component velocities (horizontal or vertical) higher than 25°/s (0.5°/per sampling frame) were eliminated from the raw eye tracking record and both horizontal and vertical components of smooth pursuit were plotted together with the appropriate component of the object motion. Figure 2 demonstrates the horizontal and vertical components of smooth pursuit during two cycles of object motion at one experimental trial in the *visible occluder* condition, plotted together with the object motion (or its component motion). The examples are from three different subjects taken from each of the three different age groups.

The gain was calculated as a ratio of the SP peak-to-peak amplitude to the object motion peak-to-peak amplitude at every half of the object's motion cycle (referred to as passage below). In the beginning and end of every movie, the first and the last quarters of the object motion cycle were excluded, leaving 15 complete object passages for the analysis. It was decided that a participant followed the motion on the display with smooth pursuit if its peak-to-peak amplitude for at least one of the above mentioned directions was greater than 20% (1°). If not, such passages were defined as attentive fixation and were not included in the later categorization of participants' SP according the direction of tracking. The timing of the smooth pursuit was calculated for every trial and for both horizontal and vertical dimensions as a median of the shift between sine approximations of the eye and object positions on the passages included in the analysis.

If the gain of smooth pursuit in the horizontal direction was greater than the gain along vertical one at the same passage, it was defined as primarily a smooth pursuit response to the *global motion* of the integrated object. If the gain of smooth pursuit in the vertical direction was greater than the gain in the horizontal direction, it was defined as primarily an SP response to the local motions

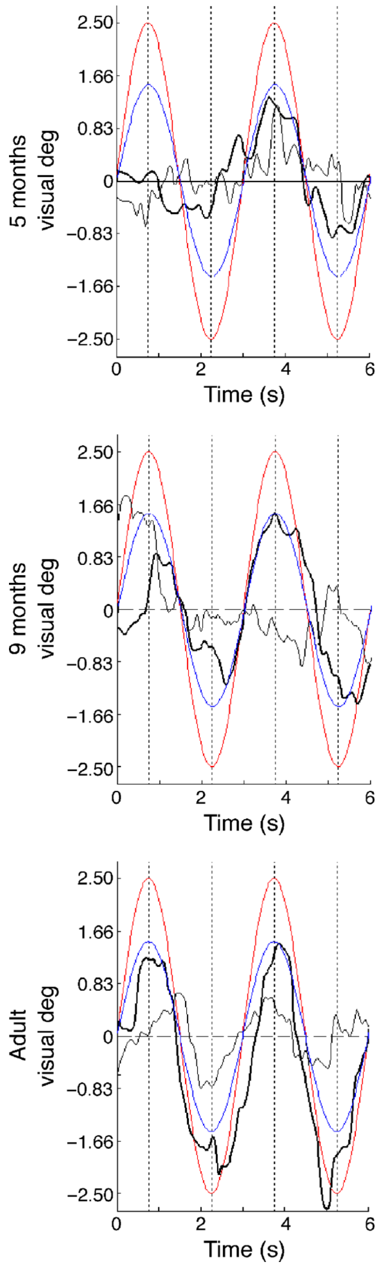

Figure 2. Two cycles of the rhombus motion tracked smoothly during a single experimental trial in the visible occluder condition. Every new cycle of the object motion started to move from the object central position. The three diagrams represent samples of data from three individual participants. The red line corresponds to the object trajectory, which was purely horizontal. The blue line indicates the vertical trajectory of one of the visible segments within the apertures. Even though the object moved horizontally, its visible segments moved vertically because of the apertures. The black solid lines represent SP eye movements: the thick one—horizontal SP and the thin one—vertical SP. The space between the vertical dotted lines corresponds to the intervals from which SP gain and lag were calculated.

of the end points of the visible stimulus segments (Beutter & Stone, 2000). In our case, their direction was always vertical, along the borders of the occluders. In other words, the smooth pursuit data were divided into 2 categories in each condition: the horizontal smooth pursuit related to the *global motion* of the integrated object and the vertical smooth pursuit related to the *local motions* of the object visible segments.

Each single attentive passage was determined to show predominantly global SP (horizontal gain of SP greater than vertical) or predominantly local SP (vertical gain of SP greater than horizontal). The number of predominantly global (local) responses relative to the number of attentive passages in a trial was then analyzed.

As can be seen above, this analysis was based on classification of the predominant direction of SP, and at the same time, it did not take into account the bias to another direction of motion. Such simplified classification could influence results, at least, by means of diminishing obtained effects. Thus, in addition to this measure, we also compared the magnitudes of raw amplitudes of SP at all attentive passages. Such comparisons were done for both horizontal and vertical components of SP and for both experimental conditions. Consequently two types of analysis were applied, one devoted to the normalized values (gain) and one to the raw values.

Results

Overall performance

All the subjects in the adult group reported that in the visible occluder condition they perceived the rhombus figure moving horizontally but not always from the beginning of the experiment. No such percept was reported for the invisible occluder condition.

Analysis of the SP pattern in all three groups of subjects showed that all participants tracked the target in both horizontal and vertical directions with SP. Figure 3 provides individual examples of smooth pursuit gaze tracking for a single experimental trial in both conditions at every age group.

Repeated measures ANOVA (2 conditions × 2 categories × 3 age groups) performed on the percentage of trials where the subjects tracked the global horizontal motion more than the vertical with SP (according to the gain-based classification of passages we described in the General methods section) showed that, in the visible occluder condition, the proportion of such trials increased with age (F (2, 52) = 6.8, $p < 0.003$, $\eta^2 = 0.22$). The 5-month-old infants showed predominantly smooth pursuit response to the global motion at around 12% of the analyzed object motion passages while the 9-month-olds did it in 20% and adults in 26% of the passages. Tukey

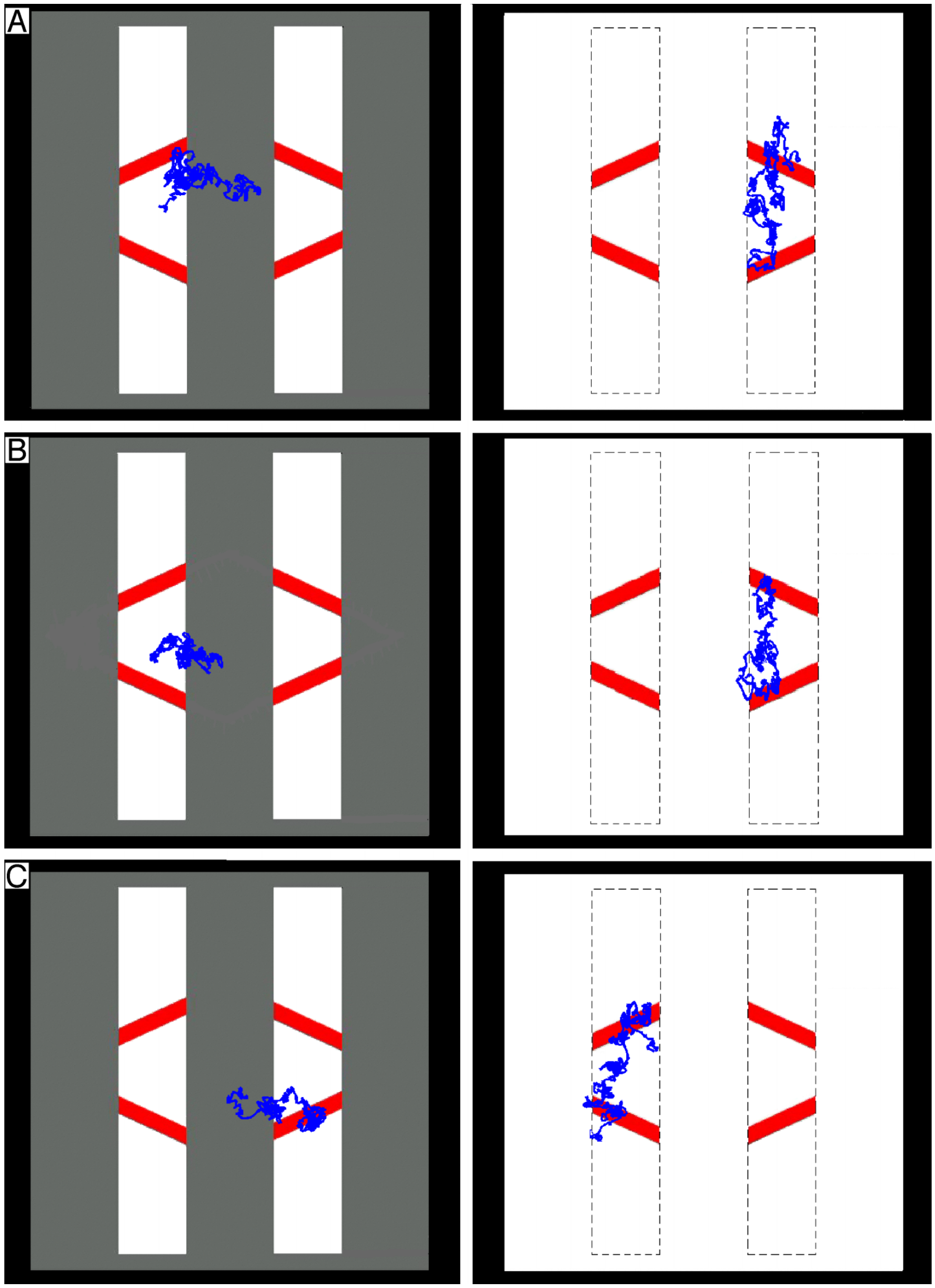

Figure 3. Individual examples of well-performed SP tracking patterns from (A) an adult, (B) a 9-month-old infant and (C) a 5-month-old infant during a full experimental trial (8 cycles) in the visible and invisible occluder conditions. *Note*: The amplitude of the rhombus motion in the horizontal direction corresponds to half of the width of the middle occluder.

HSD post hoc test revealed that this increase with age was only significant between 5 and 9 months of age ($p < 0.002$). All these effects can be seen in Figure 4. Note that the percentages of trials with predominantly horizontal and vertical pursuit do not add up to 100% because sometimes participants looked at the display but did not follow the object motion. Instead they just fixated some point on the screen in the area of the rhombus motion.

In the *invisible occluder* condition, the percentage of trials where the subjects primarily tracked the horizontal motion with SP more than the vertical did not change with age. It was 12% in 5-month-old infants, 11% in 9-month-olds and 14% in adult group (Figure 5). Furthermore there was an interaction between age and conditions (F (2, 52) = 7.3, $p < 0.001$, $\eta^2 = 0.22$). The percentage of trials where the subjects predominantly tracked the horizontal global motion with SP more than the vertical component motions did not differ between the two conditions for 5-month-old infants but did so for the 9-month-olds (Tukey HSD, $p < 0.05$) and the adults (Tukey HSD, $p < 0.011$).

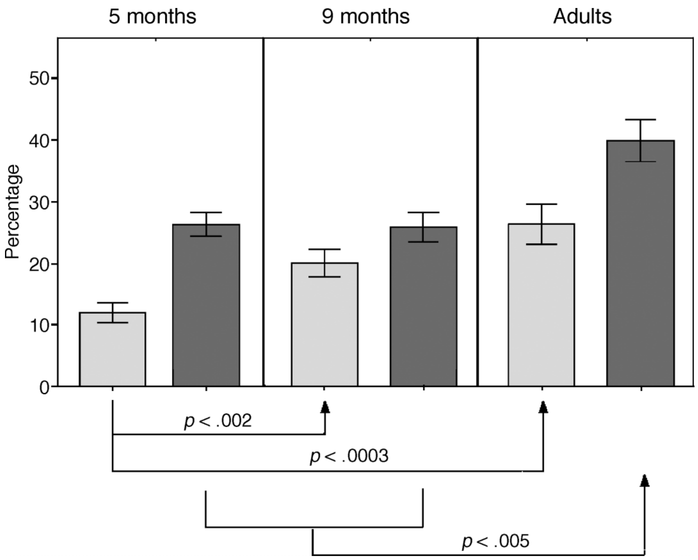

Figure 4. Average percentages and standard errors of the SP following global and local patterns in the *visible occluder condition* for all age groups. The light colored bars in every pair show average percent of the SP in the horizontal direction. The dark colored bars depict average percent of the SP in the vertical direction.

An ANOVA analysis for the *invisible occluder* condition demonstrated developmental changes in the percentage of passages where the subjects primarily tracked the incoherent motion of the separate object elements with SP. The 5-month-old infants performed primarily vertical SP at 34% of all attentive passages, the 9-month-olds did so in 42% of the passages, and the adults did so in 46% of all attentive passages. Adults were significantly better on this task than the 5-month-old infants but not better than 9-month-old infants (Tukey HSD, $p < 0.01$; Figure 5). In the *visible occluder* condition, the proportion of attentive trials with predominantly vertical SP was 26% for the 5-month-olds, 25.3% for the 9-month-olds, and 39% for the adult group. Post hoc analysis showed that the adults primarily tracked the vertical motion on a greater proportion of passages than the infant groups (Tukey HSD: $p < 0.005$).

Gain and lag of smooth pursuit

As SP is determined by perceived coherent motion, its gain and lag reflects how good this correspondence is. Thus, these measures were estimated for both horizontal and vertical SP to evaluate the relative importance of these modes of perception.

The mean gains and lags of SP with standard errors for both conditions for all three age groups are given in Table 1. A repeated measurement ANOVA (2 × 2 × 3) on the SP gains showed that there were significant differences between the age groups in the gain of smooth pursuit (F (2,54) = 6.44, $p < 0.004$, $\eta^2 = 0.19$). The gains in both the visible and invisible occluder conditions of the adult group were significantly greater compared to the gains of 5- and 9-month-old infants (Tukey HSD, $p < 0.005$). At the same time, independently of the participants' age, when subjects predominantly followed the coherent motion of the object, their gains were significantly smaller than when following the vertical motions of the object components (F (1, 54) = 72.9, $p < 0.000$, $\eta^2 = 0.57$).

All age groups showed predictive SP in both the horizontal and vertical dimensions and in both conditions. We could not detect any systematic differences in lag of SP between subjects of different age (see Table 1).

Raw amplitudes of smooth pursuit

The magnitude analysis of raw amplitudes of smooth eye movements showed results similar to the analysis of percentage of SP. We performed repeated measurement ANOVAs (2 × 2) on the raw amplitudes of vertical and horizontal SP for every trial in each condition at every age level. All three groups demonstrated significant interaction effects between the experimental conditions and quality of SP (vertical and horizontal; adults $F(1, 27) = 16.1$, $p < 0.000$; 9-month-olds $F(1, 39) = 59.1$, $p < 0.000$; 5-month-olds $F(1, 41) = 21.3$, $p < 0.000$).

Subsequent Tukey post hoc analyses revealed that the amplitudes of horizontal SP were larger in the *visible occluder* condition in comparison to the invisible one for the 9-month-olds and the adults ($p = 0.047$ and $p = 0.037$ correspondingly). For the 5-month-old infants these amplitudes did not differ ($p > 0.11$). At the same time, all three groups of subjects showed larger amplitudes of vertical SP in response to the *invisible occluder* condition than to the visible one (Tukey post hoc: 5-month-olds, $p < 0.000$; 9-month-olds, $p < 0.000$; adults, $p < 0.04$).

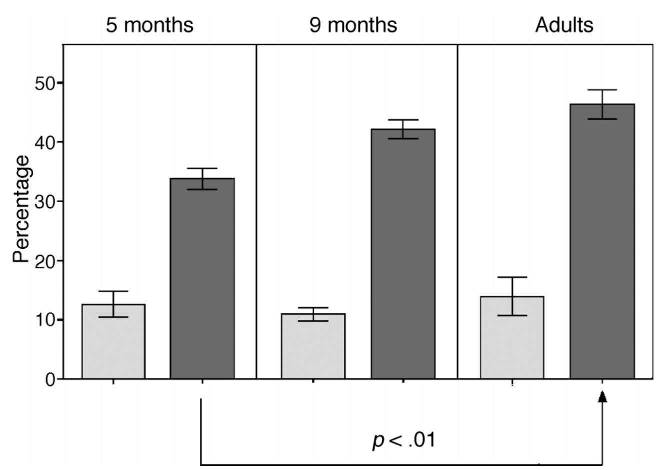

Figure 5. Average percentages and standard errors of the SP following global and local patterns in the *invisible occluder* condition for all age groups. For color symbols, see Figure 4.

	Visible occluder			Invisible occluder		
	5 m	9 m	Adults	5 m	9 m	Adults
Attentive passages	772	712	798	940	930	830
	45%	43%	50%	55%	57%	52%
Analyzed passages	289	333	483	412	522	471
	37%	47%	60.5%	44%	56%	57%
SP lag for global cues (ms ± *SE*)	−10 ± 40	−20 ± 40	−80 ± 30	−60 ± 40	20 ± 40	60 ± 80
SP lag for local cues (ms ± *SE*)	−60 ± 40	−60 ± 40	−70 ± 30	60 ± 40	−50 ± 30	−20 ± 40
SP gain for global cues (±*SE*)	0.35 ± 0.01	0.33 ± 0.02	0.43 ± 0.03	0.36 ± 0.02	0.38 ± 0.01	0.44 ± 0.03
SP gain for local cues (±*SE*)	0.39 ± 0.02	0.38 ± 0.02	0.49 ± 0.03	0.44 ± 0.02	0.45 ± 0.02	0.51 ± 0.02

Table 1. The average smooth tracking performance (SP) in both conditions for each age group. The percentage of attentive passages calculated as fraction of all presented passages. The percentage of analyzed passages is calculated as fraction of all attentive passages.

Distribution of smooth pursuit over trial

Though the average amount of SP predominantly in the direction of the global motion of the object for 5-month-old infants in the *visible occluder* condition was not statistically different from SP observed in this direction in the *invisible occluder* condition we observed differences in the distribution of the SP over single trials. In the *visible occluder* condition 5-month-olds primarily followed the global motion of the object significantly more toward the end of a trial ($F(1, 7) = 17$, $p < 0.005$, Tukey HSD, $p < 0.03$, $\eta^2 = 0.71$). At the same time, in the *invisible occluder* condition the amount of SP predominantly in the direction of global motion remained unchanged over single trials.

In the *visible occluder* condition linear regression analysis revealed, for all age groups, an increase within single trials of the percentage of global SP (see Figure 6). In the group of 5-month-olds, the linear regression model explained 34.5% of data variance ($F(1,13) = 8.4$, $p < 0.02$, $\beta = 0.63$), in the group of 9-month-olds the regression model explained 22% of data variance ($F(1,13) = 5$, $p < 0.05$, $\beta = 0.53$) and in the group of adult participants linear regression model contributed to explanation of 35.3% of data variance ($F(1, 13) = 8.6$, $p < 0.02$, $\beta = 0.63$). In other words, the longer the participants were exposed to the partly occluded moving object, the greater was the tendency for the SP to accord with the global pattern of motion.

In contrast to the increase in percentage of SP across single trials, no significant increase in the SP of the coherent object motion was observed over the whole experiment.

In response to the *invisible occluder* condition, learning effects could only be observed for predominantly vertical SP of the 9-month-old infants ($R^2_{adj} = 0.32$, $F(1, 13) = 9.3$, $p < 0.01$, $\beta = 0.65$, see Figure 6). Nine-month-old infants increased the number of passages where they primarily tracked the component moving object parts with SP along the vertical borders of the occluders.

Discussion

Perceived local motion and its integration to global motion

It was found that gain of the vertical SP dominated in all conditions indicating that the retinal slip of single motion elements is the most effective determinant of smooth pursuit at any age in the present situation. However, the dominance of vertical smooth pursuit was less striking in the visible occluder condition. Instead, significantly more horizontal smooth pursuit was elicited in this condition than in the invisible occluder condition for the 9-month-olds and the adults. These results correspond to the reported impression by the adult subjects of perceived vertical motion of single elements in the invisible occluder condition and perceived horizontal global motion of the whole figure in the visible occluder condition.

Cardinal changes in the tendency to follow the perceived integrated object with SP occur between 5 and 9 months of age. The present experiment provides evidence that 9-month-old infants can use SP to track the perceived direction of the rhombus's global motion and they can do it to the same extent as adults.

In contrast, the tendency of 5-month-olds to respond with horizontal SP in the *visible occluder* condition was highly comparable to degree they followed the global motion in the *invisible occluder* condition. Moreover, the degree of horizontal SP tracking was not statistically different from the amount observed in 9-month-olds and adults in the *invisible occluder* condition. The results indicate that cardinal changes in the tendency to follow the integrated global motion with SP occur between 5 and 9 months of age. The present experiment provides evidence that 9-month-old infants use SP to track the perceived direction of the rhombus's global motion and they do it to the same extent as adults.

Does this indicate that the ability to control SP by the global perception of a moving object is weak at 5 months

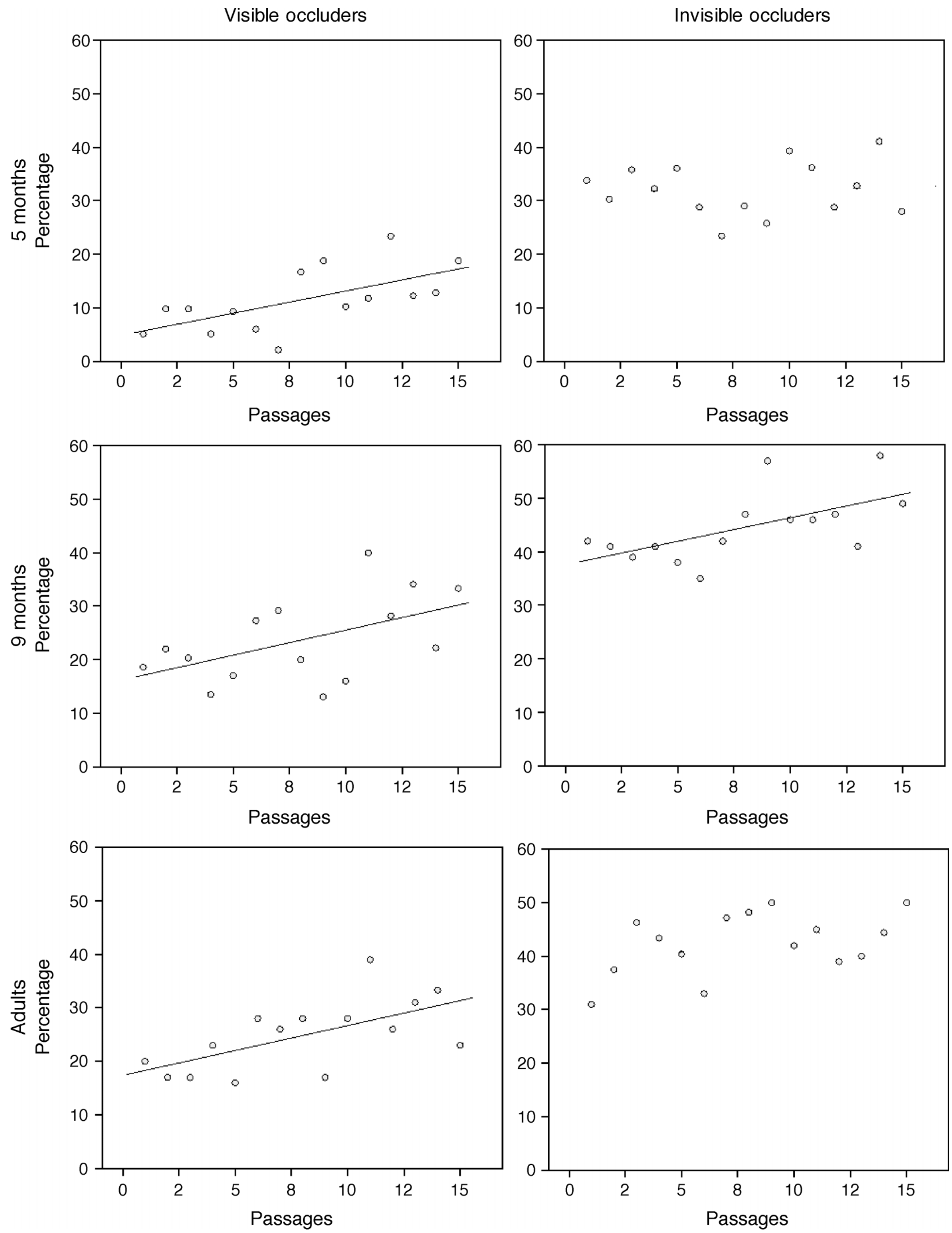

Figure 6. The fraction of smooth pursuit at every object passage over all subjects as a function of number of passages performed by infants and adults in both conditions. The left graph panel represents horizontal SP data and the right graph panel represents vertical SP data. Solid lines show statistically significant regressions.

of age? The analysis of the change in horizontal SP in the *visible occluder* condition over single trials argues for a different conclusion. All three groups of participants showed an increase in the tendency to respond with SP to the global motion of the object in the *visible occluder* condition (Figure 6). No such learning effect for horizontal SP was observed in the *invisible occluder* condition. Moreover, this learning effect is surprisingly similar for all subject groups (in spite of differences in general amount of global SP) suggesting that it reflects a basic characteristic of the visual system.

These results are important as they indicate that the ability to track global motion with smooth pursuit develops during the first year of life. It shows that the competence in smooth pursuit tracking demonstrated by young infants (Rosander & von Hofsten, 2002; von

Hofsten & Rosander 1997) is geared to the retinal slip of single motion elements. Only gradually do infants become able to gear their SP to the perceived motion of an object that is only revealed by visible fractions. This is shown by the increase in such SP with age and with experience.

Finally, the analysis of the raw amplitudes of smooth pursuit for all age groups confirmed findings of the main analysis and showed the same pattern of results.

Neurophysiological considerations

The fact that the different aged groups performed at different levels when tracking the global motion pattern with SP but showed similar tuning patterns to object coherent motion over time indicates that the visual motion is processed by the same neural substrates at all three age groups. Taken together, the results suggest that although 5-month-old infants show a very low level of SP in response to the integrated coherent object motion, it is controlled by the same mechanism as in 9-month-olds and adults. Recently, Stone and Krauzlis (2003), studying simultaneously perceptual and oculomotor responses in adults, proposed that the co-variation of the pursued and perceived directions in response to a white spot moving over a dark background provide strong evidence that perception and smooth pursuit share the same neural circuitry that computes target motion direction. This does not occur at the level of MT or earlier but at the level of MST or further downstream, because the MST area is associated with motion processing in the world-centric coordinates whereas MT area is associated with early motion processing in retinal coordinates (for review see Stone & Krauzlis, 2003). Taking this finding into account, our experiment suggests that MST is involved in control of the global SP already at 5 months of age. The process of transition from SP controlled by local displacements of the stimuli on the retina to perceived external motion of the object was time consuming for all age groups. In other words, the transition from SP based on retinal coordinates supported by the MT area (Stone & Krauzlis, 2003) to the SP control based on world-centric coordinates supported by MST area is a gradual process over time. The smooth pursuit system becomes better tuned to the perception of global motion over exposure time.

This process could either be perceptual in that the neural processes resonating to global motion are strengthened, or that the SP gets increasingly entrained by the global motion over time.

Experimental design

The experimental design of this study counterbalanced trials where global motion of the object could and could not be observed. Such design might have canceled increasing adjustment of SP to global motion over consecutive trials in the *visible occluder* condition. In other words, an increasing tendency to see global motion during a *visible occluder trial* might have been canceled during the next *invisible occluder* trial. Perhaps, the adjustment to the global motion over trials would be more profound if the experimental design had been adapted to it.

Timing

Independently of whether the infants or the adults tracked the end points of the visible segments or the coherent motion of the integrated object—their eye movements were always predictive. These results confirm the findings of von Hofsten and Rosander (1997) for smooth pursuit timing. They found that infants anticipate well-defined moving objects of various sizes. The lag of smooth pursuit to the object motion was less than 100 ms at 15 weeks of age (Rosander & von Hofsten, 2002). Thus, one can assume that it does not matter for infants if the object that they follow with smooth pursuit is small and well defined (locally) or a result of an integration of component motions. If infants are able to smoothly follow the coherent motion of an integrated object they will do it in a predictive manner.

The gain of SP

The gain of SP in the present study was lower than in earlier similar studies on adults (Beutter & Stone, 2000; Krauzlis & Stone, 1999; Stone et al., 2000). There are, at least, two possible reasons for this. First, the velocity of the presented motion was relatively low, 3.4°/s, which is only 50% of the one used by Dobkins et al. (2004), and 33% of the one used by Beutter and Stone (2000). Such a low velocity was chosen to minimize the portion of saccades and head movements in subjects' tracking pattern. The negative effect of the slow motion was a relatively low level of attention to the moving object. The gain of SP was only above 0.2 in 30% of the time for the adults and 20% of the time for the infants.

A second possible reason for sub-optimal attention was the absence of a clear instruction to attend to the motion.

In the case of tracking incoherent local motions of the visible parts of the object, the velocity of the whole object was not so critical and in this case all three groups of participants tracked them with a gain above 0.2 at around 1/3 of the time.

Conclusions

The results of this study show that the ability to track global motion with smooth pursuit develops during the first year of life. The 9-month-old infants performed such SP at an adult-like level but the 5-month-olds had significantly more difficulties in using SP in order to follow the global motion of the object. Only gradually do infants become able to gear their SP to the perceived motion of an object that is only revealed by visible fractions. This is shown by the increase in such SP with age and with experience.

Similarity of the SP increase in the direction of the global motion over exposure time in all age groups suggests that the same neural mechanisms are involved in this process for all age groups. Thus, it can be assumed that MST area starts to be involved in this process at 5 months of age but than it continues to develop, at least, over the first year of life. Significant shift, when SP starts to be influenced by world-centric coordinates, happens between 5 and 9 months of age. In addition, the observation of continuously moving visible parts of the object strengthens the SP determined by global motion in both infant and adult groups.

Acknowledgments

We would like to thank Claes von Hofsten, Oliver Braddick and Luciano Fadiga for very helpful discussions and constructive criticisms, which helped improve the paper. This work was supported by grants to Claes von Hofsten from the Swedish Research Council (2004-12172-22115-26) and EU Integrated Project (FP-004370: Robotcub).

Commercial relationships: none.
Corresponding author: Olga Kochukhova.
Email: olga.kochukhova@psyk.uu.se.
Address: Box 1225, Uppsala Se 751 42, Sweden.

References

Beutter, B. R., & Stone, L. S. (2000). Motion coherence affects human perception and pursuit similarly. *Visual Neuroscience, 17,* 139–153. [PubMed]

Braddick, O. J., Birtles, D., Cowie, D., Anker, S., Wattam-Bell, J., & Atkinson, J. (2005). *Development of local and global processing in dorsal and ventral streams: An overview*. 10th CVRS Meeting, Bled, Slovenia. http://www.cvrsoc.org/CVRS2005.pdf.

Dobkins, K. R., Fine, I., Hsueh, A. C., & Vitten, C. (2004). Pattern motion integration in infants. *Journal of Vision, 4*(3):2, 144–155, http://journalofvision.org/4/3/2/, doi:10.1167/4.3.2. [PubMed] [Article]

Johansson, G. (1950). *Configurations in event perceptions: An experimental study*. Uppsala: Almqvist & Wiksells Boktryckeri AB.

Johnson, S. P., & Aslin, R. N. (1995). Perception of object unity in young infants. *Developmental Psychology, 31,* 739–745.

Johnson, S. P., & Aslin, R. N. (1996). Perception of object unity in young infants: The roles of motion, depth, and orientation. *Cognitive Development, 11,* 161–180.

Johnson, S. P., & Nañez, J. E. (1995). Young infants' perception of object unity in two-dimensional displays. *Infant Behaviour and Development, 18,* 133–143.

Johnson, S. P., Slemmer, J. A., & Amso, D. (2004). Where infants look determines how they see: Eye movements and object perception performance in 3-month-olds. *Infancy, 6,* 185–201.

Kellman, J. P., Gleitman, H., & Spelke, E. S. (1987). Object and observer motion in the perception of objects by infants. *Journal of Experimental Psychology: Human Perception and Performance, 13,* 586–593. [PubMed]

Kellman, P. J., & Spelke, E. S. (1983). Perception of partly occluded objects in infancy. *Cognitive Psychology, 15,* 483–524. [PubMed]

Kellman, P. J., Spelke, E. S., & Short, K. R. (1986). Infant perception of object unity from translatory motion in depth and vertical translation. *Child Development, 57,* 72–86. [PubMed]

Kowler, E., & McKee, S. P. (1987) Sensitivity of smooth eye movement to small differences in target velocity. *Vision Research, 27,* 993–1015. [PubMed]

Krauzlis, R. J., & Stone, L. S. (1999). Tracking with the mind's eye. *Trends in Neurosciences, 22,* 544–550. [PubMed]

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

Lorenceau, J., & Shiffrar, M. (1992). The influence of terminators on motion integration across the space. *Vision Research, 32,* 263–273. [PubMed]

Manny, R. E., & Fern, K. D. (1990). Motion coherence in infants. *Vision Research, 30,* 1319–1329. [PubMed]

Robinson, D. A. (1965). The mechanics of human smooth pursuit eye movement. *The Journal of Physiology, 180,* 569–591. [PubMed] [Article]

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

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

Slater, A., Morison, V., Somers, M., Mattock, A., Brown, E., & Taylor, D. (1990). Newborn and older infants' perception of partly occluded objects. *Infant Behaviour and Development, 13,* 33–49.

Stone, L. S., Beutter, B. R., & Lorenceau, J. (2000). Visual motion integration for perception and pursuit. *Perception, 29,* 771–787. [PubMed]

Stone, L. S., & Krauzlis, R. J. (2003). Shared motion signals for human perceptual decisions and oculomotor actions. *Journal of Vision, 3*(11):7, 725–736, http://journalofvision.org/3/11/7/, doi:10.1167/3.11.7. [PubMed] [Article]

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

Wattam-Bell, J., Birtles, D., Braddick, O., & Atkinson, J. (2005). *Development of VEPs to global form and motion*. 10th CVRS Meeting, Bled, Slovenia. http://www.cvrsoc.org/CVRS2005.pdf.