

Stability in Young Infants' Discrimination of Optic Flow

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Although considerable progress has been made in understanding how adults perceive their direction of self-motion, or heading, from optic flow, little is known about how these perceptual processes develop in infants. In 3 experiments, the authors explored how well 3- to 6-month-old infants could discriminate between optic flow patterns that simulated changes in heading direction. The results suggest that (a) prior to the onset of locomotion, the majority of infants discriminate between optic flow displays that simulate only large ($> 22^\circ$) changes in heading, (b) there is minimal development in sensitivity between 3 and 6 months, and (c) optic flow alone is sufficient for infants to discriminate heading. These data suggest that spatial abilities associated with the dorsal visual stream undergo prolonged postnatal development and may depend on locomotor experience.

Mobile organisms must accurately determine their direction of self-motion, or *heading*, in order to control body posture, avoid collisions, and move quickly and efficiently through the environment. There are a number of potential sources of information about heading direction (Cutting, Springer, Braren, & Johnson, 1992), but one of the most important and widely studied is *optic flow*, the pattern of visual motion generated by an observer moving through a rigid environment (Gibson, 1966, 1979). Extensive empirical investigations have shown that adult observers can determine heading direction from optic flow with a high degree of accuracy (Warren, 1998). Moreover, rudimentary sensitivity to optic flow patterns simulating either an object's approach toward the face or the forward/backward motion of the observer emerges within the first several weeks and months after birth (Bertenthal & Bai, 1989; Bertenthal, Rose, & Bai, 1997; Jouen & Lepecq, 1989; Pope, 1984; Yonas, Pettersen, & Lockman, 1979). Nevertheless, there are few data describing the extent to which young infants discriminate between optic flow patterns that specify different directions of observer motion or how discrimination changes with development. The question is an important one because several authors have observed that various dimensions of spatial perception and spatial cognition undergo considerable development in the first several months of life (Atkinson, 2000; Gilmore & Johnson, 1997a, 1997b; Newcombe & Huttenlocher, 2000) that is due to, among other factors, development in processing circuitry associated with the dorsal visual processing stream and perceptual and motor experience. This article focuses on quantifying the heading direction discrimination abilities of 3- to 6-month-old infants under

different visual conditions in order to determine whether sensitivity develops prior to the onset of crawling and whether infants' sensitivity to changes in heading direction depends on optic flow alone or on other visual cues.

Adult observers can perceive heading angles of less than 1° of visual angle under a variety of circumstances (Royden, Crowell, & Banks, 1994; Warren, Morris, & Kalish, 1988). This level of accuracy is more than sufficient for locomotion across a wide range of speeds (Cutting et al., 1992). Sensitivity remains robust even when the speed of motion and the density of moving elements are varied (Warren, 1998). Moreover, the addition of vestibular or proprioceptive information associated with actual self-movement adds very little to the accuracy afforded by visual information alone (Telford, Howard, & Ohmi, 1995).

Despite a growing body of evidence about adult performance, relatively little is known about the early origins of self-motion perception. One line of research has focused on a different, but related, problem: infants' abilities to discriminate whether objects are moving toward or away from them. Studies in this area have found that rudimentary abilities to discriminate approaching from receding objects emerge in the first several weeks of life (Ball & Tronick, 1971; Yonas et al., 1979) but develop slowly over the next several months (Nañez, 1988; Nañez & Yonas, 1994; Yonas et al., 1979). Specifically, young infants appear to discriminate whether objects are approaching their faces on a collision course or will pass by them without colliding (Ball & Tronick, 1971), but little is known about the development of sensitivity to small changes in object direction.

A second line of research more closely related to the perception of heading direction focuses on the extent to which optic flow influences the control of body posture. Oscillating patterns of optic flow induce body sway in newly walking infants (e.g., Lee & Aronson, 1974). Further, rudimentary sensitivity to optic flow patterns associated with at least some types of self-motion emerges quite early. Infants in the first 2 months of life make directionally appropriate lateral head movements in response to moving stripe patterns (Jouen & Lepecq, 1989; Pope, 1984). Also, the oscillatory motion produced in a "swinging" room induces measurable body sway in infants as young as 5 months (Bertenthal & Bai, 1989; Bertenthal et al., 1997). In addition, the likelihood that body sway

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This research was conducted with financial assistance from the Pennsylvania State University and the National Science Foundation (Grant BCS-0092452). Thomas J. Baker collected a portion of these results as part of his undergraduate honors thesis. We gratefully acknowledge the assistance of Melissa Arnett and the comments of Cathleen Moore, Terri Lewis, Karen Gabel, and Mike Dahlin on the manuscript.

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will be detected at the same frequency as the visual motion increases throughout the 1st year of life, as do the amplitude and directional selectivity of body sway (Ashmead & McCarty, 1991; Bertenthal & Bai, 1989; Bertenthal et al., 1997). These data imply that the rudimentary sensitivity to optic flow associated with self-motion emerges early in infancy but undergoes considerable development over the 1st year of life.

Despite extensive data on adults' abilities to detect changes in heading and infants' sensitivity to various patterns of motion, there are few data on the question of how precisely infants can discriminate the visual information associated with different directions or speeds of self-motion. Because the acquisition of this sort of visual information is critical both for perceiving spatial layout and for a variety of locomotor behaviors such as sitting erect, crawling, cruising, standing, and walking, quantifying its early developmental origins is of considerable importance. In particular, it is important to know just how precisely young infants can discern changes in their direction of heading from optic flow in order to determine whether and how sensitivity changes and what factors shape its development.

Heading Discrimination in Infancy

Somewhat surprisingly, there is apparently only a single study in the literature that has tried to address how well young infants discriminate between displays depicting changes in heading direction from optic flow (Gilmore & Rettke, 2003). The goal in that study was to quantify how accurately 4-month-old infants could discriminate between optic flow patterns that simulated different directions of heading. Gilmore and Rettke (2003) tested sensitivity to changes in heading direction specified by optic flow using both look-time habituation and psychophysical (forced-choice preferential looking, or FPL) techniques. The results from both techniques provided convergent evidence that 4-month-olds could discriminate between displays depicting large (32° , 64° , and 180°) changes in heading direction but not small to intermediate (4° , 8° , or 16°) changes. This evidence suggested that the minimum heading-angle change that 4-month-old infants could detect in optic flow patterns was between 16° and 32° .

This study left a number of important questions unanswered. The first concerns the degree to which infants' discrimination abilities were governed by optic flow alone or were sensitive to other aspects of the visual environment associated with depth or changes in depth such as optic expansion, texture gradients, occluding and appearing contours, and shading. In other words, was the relatively poor sensitivity observed due to the absence of visual information about depth and motion in depth that is typical in natural viewing conditions? Answering this question is important for determining whether the relatively poor sensitivity found previously was specific to the random dot displays used by those authors (Gilmore & Rettke, 2003) or is a more general feature of infant vision. In other words, is optic flow alone a sufficient basis for infants' discrimination?

A second question raised but not answered by the Gilmore and Rettke (2003) study is what the smallest angle of change in simulated heading direction is that 4-month-old infants can discriminate. The study suggested that this angle lies between 16° and 32° but could not narrow the range further. Not only should this result be replicated, but determining infants' sensitivity more pre-

cisely is critical for future studies of how these abilities change later in infancy.

Finally, Gilmore and Rettke (2003) left open the question of whether there are measurable changes with age in infants' discrimination of heading direction in early infancy. On the one hand, many components of visual spatial perception, including stereopsis (Birch, Gwiazda, & Held, 1982; Held, Birch, & Gwiazda, 1980), the perception of body-centered spatial direction (Gilmore & Johnson, 1997a, 1997b), and sensitivity to pictorial depth cues (Yonas & Granrud, 1985), undergo considerable development between 3 and 6 months of age, making this a time of rapid change in visual spatial processing (Newcombe & Huttenlocher, 2000). On the other hand, some aspects of spatial vision, such as the discrimination of changes in uniform motion direction, do not seem to change substantially, at least between 3 and 4 months (Banton, Bertenthal & Dobkins, 2001). Indeed, Banton and colleagues have suggested that the development of sensitivity to *uniform* or *global* patterns of motion, such as those generated by self-motion, differs from the emergence of sensitivity to *relative* patterns of motion, such as that produced by object motion against a static background (Banton & Bertenthal, 1997; Banton et al., 2001). The differences may stem from distinct patterns of motion produced by object-versus self-motion, distinct motion processing systems in the brain, and infants' experiences with each type of motion. Thus, the question of whether heading discrimination does or does not change between 3 and 6 months can inform our understanding of both the development of low-level motion processing abilities and the role of different types of visual experience.

Infants younger than 6 months produce some optic flow patterns based on eye, head, and body movements, but until they begin to crawl they do not produce the radial patterns of optic flow associated with translational or forward motion of the observer through the environment. At the same time, infants in this age range and even older infants do experience radial optic flow patterns passively when adults carry them. Thus, if substantial development in heading sensitivity depends on active, but not passive, visual experience, there may be minimal development in this vital perceptual skill in young prelocomotor infants.

The Current Experiments

To address these issues, we conducted three experiments. The extent to which optic flow information alone is sufficient for discrimination was tested by varying the type of visual environment—a simulated ground plane in Experiment 1, a cloud of dots in Experiment 2, and a 3-D-rendered environment with multiple pictorial and motion cues to depth and movement in depth in Experiment 3. To determine more precisely the smallest change in heading angle that infants could discriminate, we selected a range of test angles different from the set tested previously and used a modified version of the FPL technique (Teller, 1979). To test for developmental trends during a time period when substantial passive experience with self-motion is likely to accumulate, we tested infants cross-sectionally across two time spans—from 3 to 5 months of age in Experiments 1 and 2 and from 3 to 6 months of age in Experiment 3. In all three experiments, control data from 1 or more adult participants were obtained to provide benchmarks against which to compare infants' performance.

Experiment 1

Method

Participants. Thirteen 3-month-old infants (8 girls; mean age = 100 days; range = 90–108 days), and 18 five-month-old infants (12 girls; mean age = 158 days; range = 152–162 days) participated. All infants were born between 37 and 42 weeks of gestation and had birth weights in excess of 2,500 g. The infants were recruited by telephone from information contained in birth announcements published in the local newspaper. A 20-year-old woman with corrected-to-normal vision who was unaware of the hypotheses of the study also participated.

Display. The display region was 40° horizontal (H) by 30° vertical (V). Within a trial, the display consisted of two computer-generated movies presented simultaneously, side by side. Each depicted translational self-motion along a simulated ground plane and was presented in a rectangular region 15° (H) by 30° (V) positioned at the far left and far right sides of the larger display. Each movie consisted of 25 individual frames presented at 30 frames/s. Each frame of the display consisted of 38 white dots (luminance = 72 cd/m²), 24 min of arc in width, presented on a black background (0.1 cd/m²). This resulted in a dot density within the region where dots were displayed of 0.17 dots/deg². The locations of the dots were chosen at random for each trial subject to the constraint that dot positions be distributed along the region of the simulated ground plane that was visible at the start of a trial. In order to reduce the tendency for dots to cluster at the virtual horizon, dot positions in 3-D were chosen by sampling from a mixed distribution: The *z* or distance coordinate for 33% of the dots was chosen from a uniform or rectangular distribution; the remainder were chosen from an inverse distribution (1/*z*). A simulated eye height of 87.5 cm and a horizon truncated at 3,800 cm were used to compute dot positions on the screen. The simulated translational speed used to compute dot displacements was a constant 5.0 m/s. This resulted in display conditions with different mean and median optical speeds and directions for each angle of motion change, as shown in Table 1. Dots that disappeared from view during a frame reappeared on the next frame at the simulated horizon in order to create the illusion of continuous motion in depth. Figure 1 shows a schematic of the display.

Each movie consisted of alternating episodes of forward and backward motion in which the direction of simulated translation changed at a temporal frequency of 1.2 Hz, or approximately every 0.83 s. During the first 1.67 s, the movies in both the left and the right windows depicted the same directions of motion—heading of 0°, then backward at a heading of 180°. During the next 1.67 s, the direction depicted in *one* of the display windows was different from zero, but the motion depicted in the other window was the same as before. The nonzero angle of motion depicted in a given trial was chosen from a constant set of angles described below. The nonzero display depicted forward motion and then backward motion along an axis different from the anterior/posterior axis depicted in the other display so that the two were synchronized in time. The pattern of presenting the same directions of simulated observer motion in the two display windows

followed by a different direction in one of the display windows continued in an alternating fashion until the observer terminated the display cycle by pressing a key.

On a single trial, each infant was shown a set of displays in which one of three nonzero angular magnitudes and one of two directions (left or right of the anterior–posterior axis) was depicted. Three-month-olds viewed motion along axes 22°, 45°, or 90° to the left or right of the anterior–posterior axis. Five-month-olds viewed motion at 12°, 22°, and 45° to the left or right of the anterior–posterior axis. On the assumption that older infants would be more sensitive to smaller angles and that younger infants might require large (e.g., 90°) heading changes in order to maintain interest, the ranges of test angles were chosen to be overlapping but not identical. The adult viewed displays depicting observer motion along axes 0.5°, 1°, 2°, 5°, and 12°. The order of the angles was random within each block of 12 trials for both infant groups (infants: 3 angles × 2 directions × 2 sides) and within each block of 20 trials for the adult (adult: 5 angles × 2 directions × 2 sides). For both infants and the adult, a single experimental episode consisted of three blocks presented continuously in a single experimental session.

Apparatus and procedure. The stimulus display was generated on a 32-in. (81-cm) Sony video monitor controlled by a Macintosh G3 computer that was running the Matlab 5.2.1 program and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) routines. The sides of the monitor were masked with dark cloth, and the entire testing apparatus was located in a quiet testing room in which the ambient lighting was dimmed. Infant participants sat in a padded infant car seat positioned so that the viewing distance was 90 cm from the center of the screen. The experimenter viewed the infant's face and eyes by means of a low-light-sensitive video camera mounted above and behind the display.

Once the infant was seated in the car seat, the experiment began. The experimenter initiated each trial with a keypress. First, a cartoon segment appeared for 2–3 s in an 8° (H) by 6° (V) window centered in the monitor. This was designed to attract the infant's attention to the center of the screen. The screen went blank and then the two optic flow movies appeared. At the end of the first 1.67 s following the start of the movie sequence, the second cycle began, in which one of the displays depicted a different, nonzero direction of motion while the other display repeated the forward/backward pattern. A message appeared directed to the experimenter indicating that she should choose the side of the display to which the infant appeared to be orienting. The message remained, and the displays were shown continuously until the experimenter made a forced choice for each trial. A keypress indicated the choice. Once the choice was made, the screen went momentarily dark, and the experimenter received feedback about whether her choice was correct before the next trial began. As deemed necessary by the experimenter to maintain interest, infants were periodically allowed to view a series of randomly positioned geometric shapes in between experimental trials. If the infant grew fussy or uncooperative, the episode was terminated.

Table 1
Optical Speed Statistics for Experiment 1 (Ground Plane) Displays

Statistic	Display condition						
	0°	3°	6°	12°	22°	45°	90°
Speed (deg/s)							
<i>M</i>	2.5	2.8	3.3	4.8	7.8	13.8	19.8
<i>Mdn</i>	1.1	1.3	1.8	2.9	5.1	9.3	13.1
Direction (degrees from vertical)							
<i>M</i>	0	26.7	51.3	73.6	81.6	86.7	90
<i>Mdn</i>	0	41.8	63.0	77.9	84.1	87.7	90

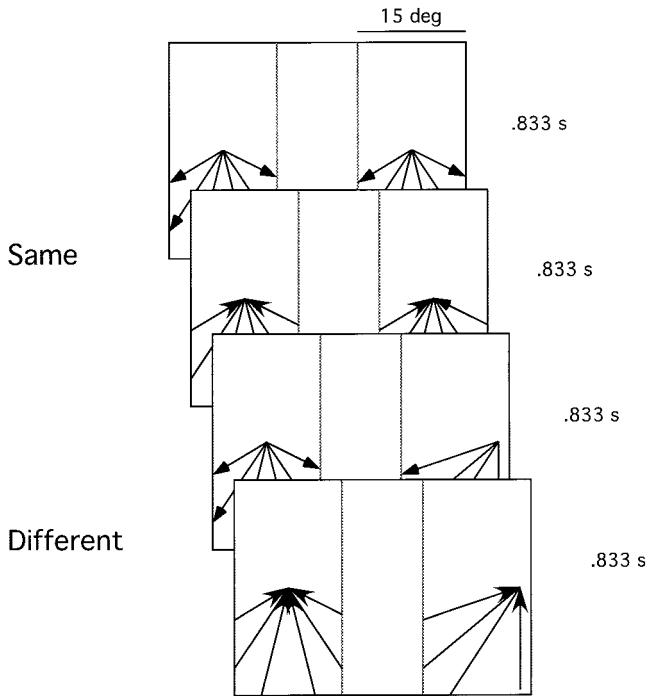


Figure 1. Schematic of the display used in Experiment 1. Two optic flow patterns appeared simultaneously in two windows on the screen. The patterns simulated forward and backward motion along a ground plane. The patterns were identical (Same) on every other forward/backward cycle. The direction of motion simulated in one of the patterns varied on the alternate (Different) cycles. The magnitude of the direction difference varied from trial to trial. See the text for additional detail.

Procedures for the adult participant were slightly different. The adult was seated in a small chair at the appropriate viewing distance and was asked to stabilize her head by holding it steady in her hands. She was then instructed to determine as quickly as possible which of the displays depicted a change in the direction of motion. The observer's task was to judge which side of the display depicted the change on the basis of the adult's eye and head movements and to press a key indicating the choice.

Data analysis. If the judgment made by the observer about the participant's side of preference matched the side on which the changing display was located, a correct response was recorded. Proportion-correct observer judgment scores for each display condition for each participant were computed. Data were collapsed across conditions that were identical in the magnitude of the heading change simulated and across side of presentation. From these data, group average proportion-correct scores were computed for each heading-angle condition. The proportions were log transformed prior to making statistical comparisons but are reported in their original units for clarity of presentation. Because a critical question of interest concerned whether infants' proportion-correct discriminations exceeded chance (.5) at different heading-change magnitudes, a series of *t* tests of mean proportion-correct scores against expected values of chance (.5) was conducted. In order to compensate for the repeated tests, a more conservative alpha level of .01 was adopted for determining statistical significance. An alternative approach would have been to conduct a mixed-design repeated measures logistic regression and report individual post hoc comparisons at each level of the independent variable of heading angle. These analyses were conducted and showed results consistent with the *t* tests, but they are not reported here for ease of exposition.

In order to compare whether group effects were representative of individual infants' performance, the proportion-correct responses observed

were compared with the expected binomial value given chance performance of .5. The number and proportion of infants whose *p* values under the binomial fell into one of three categories—less than .05, less than .1, and greater than or equal to .1—are reported.

Results

Figure 2 shows the mean (+SEM) proportion of correct judgments made by the observer as a function of the magnitude of direction simulated in the changing display. The 3-month-old group showed mean proportion-correct scores that exceeded chance levels in all three conditions: 22° ($M = .64$, $SEM = .04$), $t(12) = 3.27$, $p < .01$; 45° ($M = .71$, $SEM = .04$), $t(12) = 4.82$, $p < .01$; and 90° ($M = .68$, $SEM = .04$), $t(12) = 3.68$, $p < .01$. Five-month-olds' performance in the 12° condition ($M = .52$, $SEM = .03$) was not different from chance, but above-chance discriminations were made in both the 22° ($M = .62$, $SEM = .03$), $t(17) = 3.68$, $p < .01$, and 45° ($M = .75$, $SEM = .03$), $t(17) = 9.26$, $p < .01$, conditions. The adult's performance was above chance ($p = .5$) as evidenced by the binomial probability of the observed proportion-correct scores in both the 5° (.89) and 12° (.92) conditions.

To quantify these relationships further, we conducted an analysis of variance (ANOVA) on the infants' log-transformed proportion-correct scores with age (3 months and 5 months) as a between-subjects factor and heading angle (22° and 45°) as a within-subject factor. This analysis focused on the 22° and 45° conditions, in which both groups of infants contributed data. It showed a main effect for heading angle, $F(1, 29) = 8.61$, $p < .01$, suggesting that the proportion of correct discriminations was larger at 45° than at 22°, but no main effect for age and no interaction.

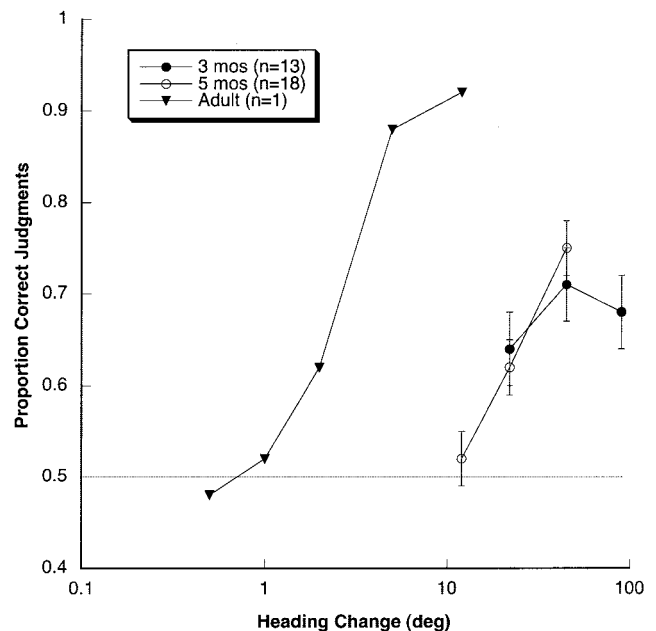


Figure 2. Data from Experiment 1: Average proportion correct judgments (+1 SEM) by heading change for the ground plane display are depicted for the adult, the 3-month-olds (3 mos), and the 5-month-olds (5 mos). Each group viewed different but overlapping sets of displays varying only in the direction of simulated motion.

In order to determine whether above-chance discriminations were observed broadly across the sample of infants, the proportion of correct responses for the combined 22° and 45° conditions for each infant was compared to the expected binomial probability under the assumption that selections were made randomly ($p = .5$). Eight of 13 three-month-olds (62%) and 14 of 18 five-month-olds (78%) had proportion-correct responses with binomial probabilities less than .1; similarly, 8 of 13 three-month-olds (62%) and 10 of 18 five-month-olds (56%) had responses with associated binomial probabilities that were less than .05. Thus, the majority of infants showed above-chance discriminations in the 22° and 45° conditions, and the proportion of infants who did not show evidence of above-chance discriminations was comparable across the two infant age groups. See Table 2 for a summary of these data across the three experiments.

Discussion

These data both replicate and extend the previous findings with 4-month-olds (Gilmore & Rettke, 2003). Both 3- and 5-month-olds discriminated between displays that depicted at least 22° changes in heading direction, but on the basis of the chance performance at 12° in the older group, it appears that changes smaller than 22° could not be discerned. Further, the data provide no evidence that sensitivity to direction-changes in optic flow patterns improves between 3 and 5 months. Mean proportion-correct values at the intermediate angles tested did not differ between the groups, nor did the proportions of infants whose individual performance suggested above-chance responding differ. Combined with the earlier results that used both a looking-time habituation/recovery method and the modified form of the FPL technique (Gilmore & Rettke, 2003), these data suggest that although rudimentary sensitivity to optic flow specifying different directions of self-motion emerges early in life, considerable development must occur after 5 months of age. The adult's performance was somewhat lower than adult performance demonstrated with other procedures, but some variability is expected given differences in display size, complexity, and the use of the forced-choice looking procedure.

The lack of evidence for changes in sensitivity between 3 and 5 months may seem surprising given other changes in visual processing that occur in this critical time period, but as mentioned earlier, it is consistent with other psychophysical results that have shown minimal development in infants' sensitivity to direction

changes in patterns of uniformly moving dots (Banton et al., 2001) during comparable time periods. Although optic flow is globally nonuniform, it is usually locally uniform in speed and direction, at least when there are a small number of static surfaces in the visual environment. Indeed, Banton and Bertenthal (1997) have argued both on behavioral and neurophysiological grounds that there may be different developmental trajectories associated with the perception of uniform motion and relative motion. Certainly, ideal observer models of adults' perception of heading direction emphasize the importance of detecting precisely the direction of local motion in order to determine the global pattern (Crowell & Banks, 1996). Thus, it is possible that sensitivity to local changes in direction may be an important factor in understanding infants' performance in the current experiments, which employed locally uniform, but globally nonuniform, patterns of flow. Experiments 2 and 3 address this point.

Because ground plane displays are only one example of the sort of optic flow a moving observer would typically encounter and ground plane displays restrict stimulation to the lower visual field, we conducted a second experiment. This experiment explored whether sensitivity would change under conditions in which optic flow was presented in both the upper and lower visual fields by means of displays that simulated motion through cloudlike patterns of dots. A second distinguishing characteristic of the displays was that, unlike the displays in Experiment 1, the cloudlike patterns of dots did not specify any particular surface structure. Analogous performance in the two experiments would attest to the generalizability across viewing situations of young infants' visual abilities to detect changes in optic flow specifying heading changes.

Experiment 2

Method

Participants. The participants were 19 three-month-old infants (8 girls; mean age = 98 days; range = 92–105 days), and 14 five-month-old infants (7 girls; mean age = 158 days; range = 150–168 days). Three young adults with no reported visual impairments also participated.

Display. The stimuli were similar to those in Experiment 1 with the following exceptions. Computer-generated movies depicted translational motion through a cloudlike pattern of dots presented so that the dot density within the display region was the same value (0.17 dots/deg²) as that in Experiment 1. The locations of the dots were chosen at random for each trial from a uniform distribution in x , y , and z , with the maximum distance

Table 2
Proportions of Infants Who Made Above-Chance Discriminations at 22° and 45°

Experiment and age group	Binomial probability of observed "correct" responses		
	$p \leq .05$	$.05 < p \leq .10$	$p > .10$
Experiment 1			
3 months ($n = 13$)	.62	.00	.38
5 months ($n = 18$)	.56	.22	.22
Experiment 2			
3 months ($n = 19$)	.42	.16	.42
5 months ($n = 14$)	.36	.21	.43
Experiment 3			
3–4 months ($n = 19$)	.84	.05	.11
5–6 months ($n = 10$)	.70	.20	.10

in z fixed at a simulated 3.8 m from the viewing plane. Adults were tested on four angle conditions (1°, 2°, 5°, and 12°). Figure 3 shows a schematic of the display.

Apparatus and procedure. The apparatus and procedure were the same as those in Experiment 1.

Results and Discussion

Figure 4 shows the mean (+SEM) proportion of correct judgments made by the observer as a function of the magnitude of direction simulated in the changing display. Three-month-olds showed above-chance performance in all three angle conditions: 22° ($M = .59$, $SEM = .02$, $t(18) = 3.78$, $p < .01$; 45° ($M = .61$, $SEM = .03$, $t(18) = 4.29$, $p < .01$; and 90° ($M = .69$, $SEM = .03$, $t(18) = 6.91$, $p < .01$). Five-month-olds showed chance performance at 12° ($M = .53$, $SEM = .05$) but above-chance discrimination at 22° ($M = .57$, $SEM = .02$, $t(13) = 3.02$, $p < .01$, and 45° ($M = .62$, $SEM = .04$, $t(13) = 3.18$, $p < .01$). A 2 (months: 3 or 5) by 2 (angle: 22° or 45°) ANOVA examining the log-transformed proportion-correct scores in the 22° and 45° conditions found no effects for heading angle or age and no interaction. Finally, 11 of 19 three-month-olds (58%) and 8 of 14 five-month-olds (57%) showed proportion-correct scores with associated binomial probabilities of less than .1; 8 of 19 three-month-olds (42%) and 5 of 14 five-month-olds (36%) had scores with associated binomial probabilities less than .05. Mean adult performance was not different from chance (.5) at 1° ($M = .55$, $SEM = .2$) but exceeded chance in the 2° ($M = .75$, $SEM = .08$), 6° ($M = .88$, $SEM = .11$), and 12° ($M = .97$, $SEM = .03$) conditions.

These results suggest that, as in Experiment 1, infants discriminated between optic flow patterns when the heading angles sim-

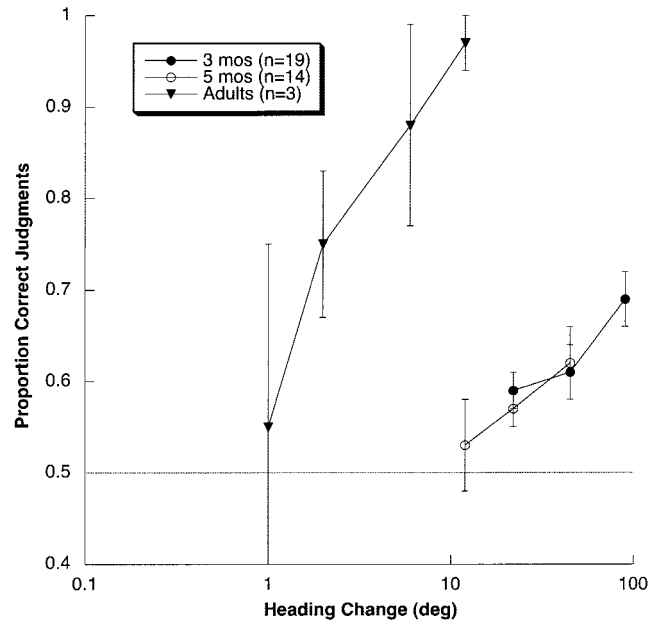


Figure 4. Data from Experiment 2: Average proportion correct judgments (+1 SEM) by heading change for the cloud display are depicted for the adult observers, the 3-month-olds (3 mos), and the 5-month-olds (5 mos).

ulated were 22° or larger. Unlike in Experiment 1, however, average proportion-correct judgments did not significantly increase as a function of heading angle, and the fraction of infants whose individual proportion correct scores for the 22° and 45° conditions exceeded chance was smaller than in Experiment 1. This suggests that despite the increase in the number of dots and the positioning of visual stimulation in both the upper and lower visual fields, discrimination was somewhat more difficult for the cloudlike displays, which contained no surface information, than for the ground plane displays of Experiment 1, which did. This implies that infants may be more sensitive to heading information in visual displays in which information about surfaces is present.

Another reason for the difference between the results may be a low-level motion cue that might have boosted infants' sensitivity in Experiment 1 but not Experiment 2: the mean direction vector. Tables 1 and 3 summarize the speed and direction statistics for Experiments 1 and 2, respectively. In the ground plane display, the mean direction of the forward or 0° condition was a vector pointing downward, whereas the mean direction of the forward 45° condition, for example, was 86° to the left or right. Accordingly, participants in Experiment 1 might have responded to the change in mean direction, not the position of the inferred focus of expansion. Data from Banton and colleagues (2001) suggest that 12-week-old infants, comparable to the 3-month-olds tested here, discriminate direction changes of 22° in uniformly moving patterns. So it seems plausible to argue that young infants could have discriminated between the displays of Experiment 1 on the basis of comparisons between the mean direction vectors in the forward (0°) condition and the nonzero conditions.

Unfortunately, this argument does not hold up under closer scrutiny. The mean direction cue was not available to the same

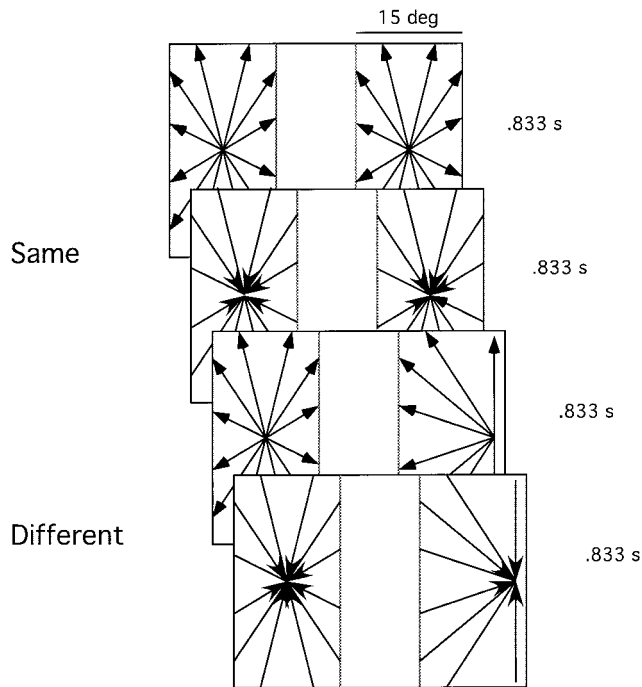


Figure 3. Schematic of the cloud display used in Experiment 2.

Table 3
Optical Speed Statistics for Experiment 2 (Cloud) Displays

Statistic	Display condition						
	0°	3°	6°	12°	22°	45°	90°
Speed (deg/s)							
<i>M</i>	3.1	3.3	3.8	5.2	7.9	13.9	19.5
<i>Mdn</i>	2.1	2.2	2.5	3.5	5.3	9.2	13.1
Direction (degrees from vertical)							
<i>M</i>	—	90	90	90	90	90	90
<i>Mdn</i>	—	90	90	90	90	90	90

Note. Dashes indicate that these statistics are undefined at this level of the display.

extent in Experiment 2 as it was in Experiment 1. In Experiment 2, as a result of the vertical symmetry of the display, mean direction in the forward 0° condition was the zero vector, whereas the mean direction in the 12°, 22°, 45°, and 90° displays was 90° to the left or right. Consequently, mean direction could have been used to discriminate between the zero and nonzero heading-angle conditions, but not between the different nonzero heading displays. The lack of a significant increase in proportion-correct judgments by heading angle in Experiment 2 supports the notion that infants might have discriminated between the displays on the basis of an essentially categorical perception of the change in the mean direction vector from 0° to 90°. However, this account fails to explain why 5-month-olds did not detect the large, greater than 70° changes in the mean direction vector in the 12° heading condition in *either* experiment. On the one hand, the lack of change in uniform direction sensitivity from 12 to 18 weeks is consistent with the lack of development in heading direction sensitivity indicated in Experiments 1 and 2. On the other hand, it is difficult to account for the pattern of results across Experiments 1 and 2 on the basis of the idea that infants converted globally nonuniform patterns of motion into mean direction vectors and compared among them at the same level of sensitivity they showed for locally uniform motion. Thus, the relationship between infants' sensitivity to changes in uniform motion direction, at least as tested by Banton and colleagues (2001), and sensitivity to changes in heading direction may be a complicated one.

To address these issues and the possibility that the presentation of optic flow patterns alone underestimated infants' abilities in both experiments, we decided to create new visual displays that more closely simulated the complex pattern of motion and surfaces characteristic of real visual environments. The displays consisted of 3-D full-color-rendered surfaces and objects placed on a simulated surface and in front of a textured background. As a result, the displays incorporated a rich array of pictorial cues to depth and motion in depth that are characteristic of natural scenes—optic expansion, contour accretion and deletion, shading, shadows from a fixed light source, and distance from the horizon. In addition, we decided to expand the age range by including 6-month-old infants in the sample.

Experiment 3

Method

Participants. Participants were 29 three- to six-month-old infants (8 three-month-olds; 11 four-month-olds; 2 five-month-olds; and 8 six-

month-olds; 12 girls). Four young adults with no reported visual impairments also participated.

Display. Movies simulating motion through a 3-D environment along different directions of motion relative to the viewing position were generated with a computer animation and rendering program (Bryce 3D). The environment consisted of an array of 15 yellow cylinders (bars) positioned in three rows of five at simulated distances of approximately 5, 10, and 15 m from the viewpoint. The bars were positioned in front of a gray and black patterned wall and atop a red and white striped ground surface. Each movie consisted of 30 frames and, like the displays in the previous experiments, was displayed in two 15° (H) by 30° (V) windows positioned at the far left and far right of the 40° (H) by 30° (V) display region. The movies were presented at 20 frames/s and, as in Experiments 1 and 2, depicted forward and backward motion along an axis to the left or the right chosen from the following subset of angles: 0°, 3°, 6°, 12°, 22°, 45°, and 90°. All movies began with a forward/backward cycle of 0° heading. Figure 5 shows a static view of the display. We attempted to estimate the average visual speed of the display by measuring the displacement in each frame shown by a sample of the visible bars. Those estimates suggested that the average optical speed ranged from 20 deg/s in the 90° heading condition to 1.8 deg/s in the 3° heading condition. We did not attempt to estimate the mean direction vector, in part because of the ambiguity concerning what exactly constituted an identifiable point. Nevertheless, because the displays included both a ground surface and visual information in both the upper and lower visual fields, the types of low-level motion cues present in both Experiments 1 and 2 should have been available in these displays.

Design, apparatus, procedure, and analysis. The design, apparatus, procedure, and analysis were the same as those in Experiments 1 and 2 with

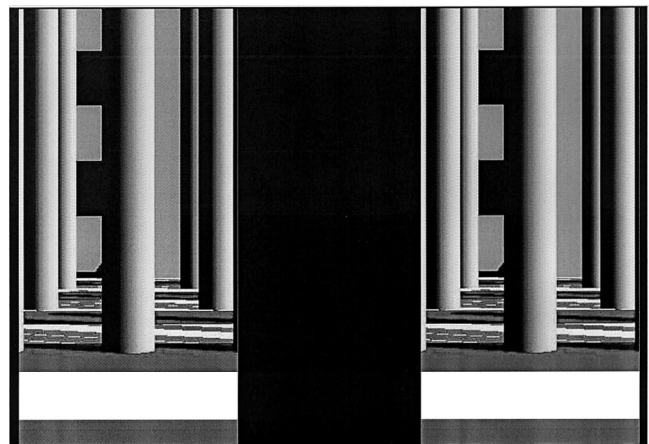


Figure 5. Static image of the "bars" display used in Experiment 3.

the following exceptions. Three- and 4-month-old infants viewed optic flow patterns at 22°, 45°, and 90°; the 5- to 6-month-olds viewed 12°, 22° and 45° patterns; and the adults viewed 3°, 6°, 12°, and 22° patterns. Some infants visited twice within a 1-week period, and the data from both visits were collapsed for analysis. Furthermore, because there was no evidence of age effects in the previous studies, we collapsed the infant sample across age for presentation and for most of the reported analyses.

Results and Discussion

Figure 6 shows the mean (+SEM) proportion-correct judgments. Three- to 4-month-olds showed above-chance performance at all three angle conditions: 22° ($M = .69$, $SEM = .03$), $t(18) = 7.52$, $p < .01$; 45° ($M = .71$, $SEM = .04$), $t(18) = 6.07$, $p < .01$; and 90° ($M = .75$, $SEM = .03$), $t(18) = 7.47$, $p < .01$. Five- to 6-month-olds showed chance performance at 12° ($M = .49$, $SEM = .03$), $t(9) = 0.03$, *ns*, but above-chance discriminations at 22° ($M = .68$, $SEM = .03$), $t(9) = 5.79$, $p < .01$, and 45° ($M = .69$, $SEM = .03$), $t(9) = 7.59$, $p < .01$. A 2 (angle: 22° or 45°) by 2 (age: 3–4 months or 5–6 months) ANOVA examining the log-transformed proportion-correct scores in the 22° and 45° conditions found no effects for heading angle or age and no interaction. Eighteen of 19 (84%) 3- to 4-month-old infants showed proportion-correct scores with associated binomial probabilities less than .1, whereas 16 of 19 (84%) infants in this age range had scores with associated binomial probabilities of less than .05. Similarly, 9 of 10 (90%) five- to six-month-olds had scores with binomial probabilities less than .1, with 7 of 10 (70%) of them having binomial probabilities less than .05. The adults showed above-chance discrimination at the lowest heading angle tested, 3° ($M = .77$, $SEM = .07$), $t(3) = 3.81$, $p < .05$, and at 6° ($M = .96$, $SEM = .02$), 12° ($M = .96$, $SEM = .04$), and 22° ($M = .96$, $SEM = .04$), all $t_s > 11$ and $p_s < .01$.

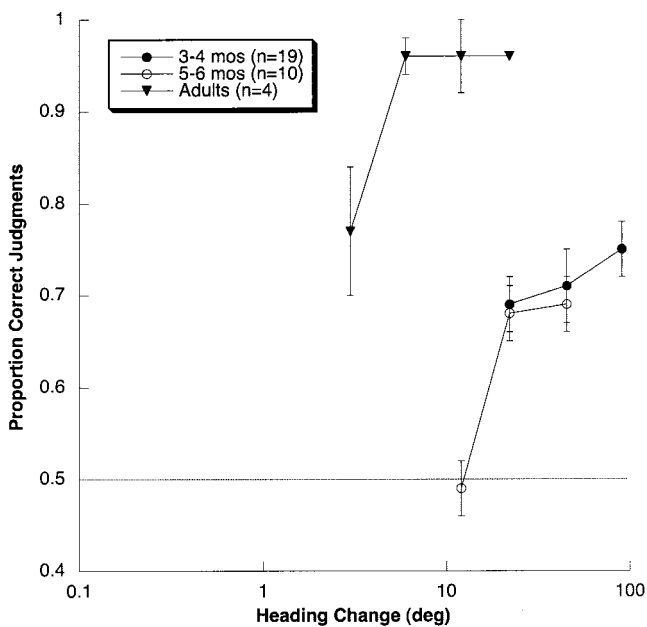


Figure 6. Data from Experiment 3: Average proportion correct judgments (+1 SEM) by heading change for the “bars” display are depicted for the adult observers and the infants separated by age group (mos = months).

These results are comparable to those from the previous experiments. Again, infants discriminated between the optic flow displays when the angle of heading simulated was 22° or larger, but there was no clear evidence that sensitivity increased substantially as a function of heading angle beyond 22°, nor was there evidence for changes in sensitivity with increasing age. The proportion of infants whose individual proportion-correct responses to the 22° and 45° conditions exceeded chance levels was higher in Experiment 3 than in the previous experiments, but this boost in performance did not extend to the 12° condition. Further, the fact that infants discriminated these visually rich displays in terms comparable to the simpler displays of the previous experiments suggests that those experiments did not underestimate infants’ abilities in this particular paradigm. Indeed, although performance in Experiment 3 was somewhat higher overall, the pattern of comparable performance across the experiments implies that infants are sensitive to multiple visual cues that accompany changes in the direction of observer motion, that infants can extract this information under a variety of circumstances, and that optic flow alone is sufficient for this type of discrimination.

General Discussion

In three separate experiments using different types of optic flow displays, 3- to 6-month-old infants’ abilities to discriminate between optic flow displays that simulated different directions of self-motion were examined using a modified form of the FPL procedure. In Experiment 1, sensitivity to displays that simulated motion parallel to a ground surface was examined, whereas in Experiment 2, sensitivity to displays that simulated motion through a cloudlike array was studied. In Experiment 3, sensitivity to displays that simulated motion in a 3-D virtual environment that depicted multiple cues to depth was examined. Despite substantial differences between the displays, the results of this series of experiments were similar. The majority of infants discriminated between displays when heading changes depicted were larger than 22°, but they did not discriminate 12° changes.

The results help resolve the questions raised by a previous study (Gilmore & Rettke, 2003). The relatively poor sensitivity found in that study was confirmed not to be specific to its displays; rather, it appears to be a general characteristic of infant behavior in both habituation and FPL-type tasks. Moreover, the roughly consistent performance across display types in the present study suggests that optic flow alone is a sufficient basis for infants’ discriminations even when surface information is absent and that displays with surface information and additional cues to depth boost sensitivity only modestly. Also, it now appears that the smallest angle of heading change 3- to 6-month-old infants can reliably discriminate appears to be between 16° and 22°, an angle large relative to adults’ performance and one not readily predicted on the basis of other data related to infants’ sensitivity to uniform motion. Finally, the results from all three experiments point to the conclusion that sensitivity to heading change as measured by the FPL technique does not develop to a measurable extent between 3 and 6 months. Coupled with earlier data obtained with both habituation and FPL methods with 4-month-old infants (Gilmore & Rettke, 2003), the current data suggest that the adultlike visual discrimination of self-motion information from optic flow develops later in infancy or childhood.

Of course, these studies share with most research in infant perception the weakness that infants' sensitivity might have been underestimated for various methodological reasons. We address these in turn.

Limitations Associated With Modified FPL

The original version of the FPL task was devised by Teller (1979) and colleagues to measure absolute grating acuity thresholds. In that version, the "choice" presented to the infant observer is between orienting toward a blank field versus orienting toward one in which a grating at a designated spatial frequency and contrast appears. Experimenters who adopt FPL assume that infants will, all things being equal, prefer to look at something rather than at a blank field in which no pattern appears. In the modified version used here, both sides of the display contain visual stimulation. One of the sides presents stimulation in which the heading angle changes, and the other simulates motion along the same, unchanging visual axis. The assumption here is that infants will prefer to look at the changing display rather than the constant display. This change makes FPL useful for measuring difference thresholds in addition to the absolute thresholds that it was originally designed to measure. Indeed, other investigators have recently extended FPL in ways similar to those in the current experiments (Chien, Palmer, & Teller, 2003). However, because infants are not instructed about which side is "correct" from the observer's point of view nor are they rewarded for looking at the changing side, one should interpret the thresholds derived from the modified FPL task cautiously. Infants' performance might be underestimated relative to a situation in which there is no choice with regard to which of two sources of stimulation toward which to orient. This clearly makes the problem of interpreting infant difference or choice thresholds more difficult, both in the current context and more broadly.

Cue Conflict

The present experiments may have underestimated infants' performance by testing them in a situation in which visual motion cues conflicted with other sensory information specifying a static observer. Infants may indeed require these additional cues, but in laboratory settings with adults, the addition of vestibular or proprioceptive information adds very little to the accuracy of self-motion perception beyond that afforded by visual information alone (Telford et al., 1995). Future studies that test infants' sensitivity to optic flow under conditions of actual self-motion would be useful in addressing this issue.

Position and Size of Stimulus Region

Infants' abilities might have been underestimated by the presentation of relatively narrow optic flow patterns in the central part of the visual field. There is some evidence that infants in a moving-room situation respond most strongly to lateral movement of the side walls (Bertenthal & Bai, 1989), and several investigators have suggested that peripheral visual information dominates postural compensation mechanisms (e.g., Held, Dichgans, & Bauer, 1975). On the other hand, more recent research with adults suggests that optic flow presented in the center of the visual field

induces postural sway that is at least as large as that induced by peripheral flow (Bardy et al., 1999; Stoffregen, 1986). Moreover, judgments of heading are more accurate with radial flow fields presented in the center of the visual field, such as the kind presented in the current infant experiments, than with lamellar flow fields presented in the periphery, such as those typically generated in the moving-room situation (Crowell & Banks, 1993). Given that an enlargement of the effective visual field is one of the characteristic patterns of early visual development (Sireteanu, 1996), it is unlikely that simply presenting the same optic flow patterns in the periphery would have improved infants' performance in the current experiments. It is possible, however, that presentation of optic flow patterns that encompassed a larger portion of the visual field would have improved discrimination performance. How much so is not known.

Visual Discrimination Versus Postural Sway

The visual discrimination measure used here might have underestimated infants' abilities relative to measures based on body movements that engage the postural control system, such as those used by other investigators (Bertenthal et al., 1997). Unfortunately, previous studies of infants' sensitivity to optic flow have not systematically varied the direction of simulated visual motion, nor is there extensive evidence about the extent to which adults match the angle of body sway to visual stimulation that simulates motion along different axes. Studies with adults do suggest that the angle of body sway changes in accord with the simulated angle of self-motion under conditions of simulated locomotion (Bardy et al., 1999). But these studies also show that it is quite difficult to detect small ($< 30^\circ$) changes in body sway because of biomechanical factors and the noise inherent in the posture signal. For similar reasons, it is likely that small systematic changes in body position in response to small changes in the heading angle specified by visual information would be especially difficult to detect in young infants even if they were produced. As a result, the visual discrimination measure is unlikely to be substantially less sensitive than are postural measures and, indeed, may be more sensitive.

Did Infants Actually Discriminate Heading?

The current experiments may not have tapped infants' abilities to discriminate heading direction per se but may instead have provided other cues to which infants responded. For example, as mentioned previously, infants might have discriminated between the displays in Experiments 1 and 2 on the basis of relatively low-level factors including optical motion statistics, such as the speed or direction of the moving elements. As Tables 1 and 3 indicate, the mean and median optical speeds of the displays in Experiments 1 and 2 differed among the control (0°) and comparison conditions. This difference stemmed from the decision to equate the speed of translational motion in 3-D space simulated by our displays. In essence, we elected to generate displays in which only the *direction* of translational motion differed, thus isolating heading change. However, this had the effect of creating optic flow patterns that differed in optical speed as a function of change in simulated heading, thus providing a potential cue infants might have used to discriminate among the displays.

The minimum (~ 5 deg/s) and maximum (~ 12 deg/s) speeds detectable by 8–10-week-olds in random dot patterns indicate performance an order of magnitude worse than that of adults (see review by Wattam-Bell, 1996). By 15–20 weeks, infants are sensitive to uniform motion at up to 30 deg/s, but sensitivity remains substantially below adult levels. Unfortunately, there is minimal evidence about the development of velocity sensitivity in infants older than 15–20 weeks. The existing data suggest that there are developmental changes from 8 to 26 weeks in the gain of smooth pursuit and the amplitude of corrective saccades made toward targets of increasing optical speed (Richards & Holley, 1999). These changes suggest that infants show improvements in their ability to adjust eye movement patterns in accord with different optical speeds. Also, Banton, Bertenthal, and Seaks (1999) showed that 6- and 18-week-old infants produced different optokinetic responses when the mean optical speed was held constant but the speed was perturbed with noise. This finding implies that infants can differentiate among displays that have subtle differences in their statistics of visual motion. What is not known is whether 3- to 6-month olds could have discriminated between the displays in the current experiments on the basis of the small changes in mean or median optical speed alone. Addressing this question is important but difficult. Although it is possible in principle to generate displays that attempt to equate or specify mean or median optical speed across a range of simulated heading angles, doing so would raise additional questions about whether infants are discriminating changes in their speed of self-motion, changes in the direction of self-motion, or both. Optical speed is relatively unimportant in the perception of heading in adults according to some ideal observer models (Crowell & Banks, 1996), but additional research is necessary to determine what role mean or median optical speed plays in infants' discrimination of optic flow patterns.

It is also possible that infants were discriminating between the displays on the basis of differences between the mean or median optical direction. The results of Experiment 2, in which all of the nonzero headings had the same mean direction vector, and those of Experiment 3, in which additional cues were provided beyond optic flow, undermine the argument that infants' performance was based largely or solely on low-level motion statistics. Nevertheless, because uniform direction sensitivity was not tested for each infant, the contribution of these variables to discrimination of optic flow patterns in infants remains to be explored. Ideal observer models mentioned previously (Crowell & Banks, 1996) suggest that low-level direction selectivity plays a central role in heading perception in adults, so comparing low-level motion sensitivity to optic flow discrimination could be quite important for a complete understanding of how optic flow perception develops in infants even if the current experiments leave the question unresolved.

On the other hand, texture accretion and deletion patterns are a low-level cue that might have influenced infants' performance in all three experiments. One unintended feature of the displays was the fact that the pattern and rate of the texture accreted or deleted at the edges of the display window were different in the different conditions. In the 0° heading condition in all of the experiments, texture accretion and deletion were symmetric on the left and right sides of the display. In the nonzero heading conditions, texture was accreted from one side and deleted from the other side. As a result of different optical speeds, the rates of accretion and deletion also varied across conditions. Others have shown that young infants

detect patterns of texture accretion and deletion (Granrud et al., 1984; Kaufmann-Hayoz, Kaufmann, & Stucki, 1986). Accordingly, it is possible that infants discriminated between the displays in these experiments on the basis of the symmetry or changes in the rate of texture accretion and deletion. The fact that the asymmetry cues in the 12° heading conditions did not lead to above-chance discrimination casts doubt on the possibility that symmetry or texture accretion and deletion fully account for the results, but a resolution of the issue will have to await additional data. Ultimately, it is important to emphasize that the perception of heading direction in adults depends on multiple combinations of low-level and high-level cues (e.g., Cutting et al., 1992; Li & Warren, 2002; Rushton, Harris, Lloyd, & Wann, 1998; Warren, 1998), so it is likely that infants are also developing sensitivity to more than one source of information in discriminating between visual displays that simulate self-motion. Thus, texture accretion and deletion may be a source of information for which sensitivity emerges relatively early.

Alternatively, there are other cues to depth or motion in depth that may not influence behavior until later and thus may contribute to the relatively slow development in sensitivity to heading information observed in the current set of experiments. For example, Yonas and colleagues have shown that sensitivity to some of the pictorial cues to depth included in the displays of Experiment 3 may not be available to the majority of 5- to 6-month-old infants (Yonas, Elieff, & Arterberry, 2002). What role pictorial information, traditionally described as being useful in static conditions, plays in the perception of self- or object motion remains an open question. Still, the fact that sensitivity to pictorial information about depth has a prolonged developmental time course may account in part for its minimal impact on performance in Experiment 3.

Implications

Two of the most intriguing questions raised by this research are how heading perception develops and when. Closely related to these questions is the relationship between perceptual development and motor development. Locomotor activity has been shown to play an important role in shaping young animals' abilities to perceive and act on some sources of visual information (Adolph, 1997, 2000; Bertenthal & Bai, 1989; Bertenthal, Campos, & Kermoian, 1994; Bertenthal et al., 1997; Held & Hein, 1963) but not others (Arterberry, Yonas, & Bensen, 1989). Thus, the finding that prelocomotor infants do not show developmental changes in heading sensitivity argues against the idea that "passive" or incidental visual experience plays more than an enabling or maintenance function with respect to this particular perceptual subsystem. Certainly, the well-known demonstration that self-produced motion was superior to its passively experienced equivalent (Held & Hein, 1963) in shaping the normal perceptual and motor development of kittens implies that there should be minimal development of sensitivity to heading direction in prelocomotor infants. The current experiments actually tested this prediction by examining the baseline levels of sensitivity to heading change in young infants who experienced optic flow associated with self-motion passively.

On the other hand, locomotor experience may not influence the emergence of sensitivity to other spatial variables such as linear perspective or texture gradients (Arterberry, Yonas, & Bensen,

1989), which, along with sensitivity to other static sources of information about depth, is thought to emerge later in infancy (Yonas et al., 2002). Moreover, the extent to which optic flow sensitivity develops as infants begin to move from experiencing optic flow largely through being moved by others to experiencing optic flow as a result of their own movements remains to be explored.

Nevertheless, the results of the current experiments are clear: (a) A crude sensitivity to relatively large changes in heading direction emerges by 3 months of age in most infants, and (b) passive visual experience accumulated up to 6 months of age changes average sensitivity very little. Whether differences in prelocomotor infants' passive experience contribute to individual differences in rates of development is an intriguing but as yet unanswered question. A related question is whether passive experience serves mainly to sustain a minimum level of perceptual sensitivity that is necessary for the onset of a later motor milestone such as sitting or crawling. This level of heading sensitivity serves as the starting point for subsequent, more rapid development that is driven largely by active experience. Data on the relationship between heading sensitivity and locomotor milestone onset would help to resolve these questions, as would data on the development of sensitivity in older infants, both of which we are collecting in ongoing work. In the meantime, the systematic exploration of infants' sensitivity to heading information illustrated here provides a new tool for examining an old but largely unexplored problem—the joint relationship between visual perception and motor development in infancy.

Similarly, the development of sensitivity to heading direction may prove to be a useful “marker” task for the development of brain circuits dedicated to high-level motion processing, like other tasks used to study visual attention (Johnson, 1990), memory (Nelson, 1995) or static spatial representation (Gilmore & Johnson, 1997a, 1997b). Neurophysiological studies have shown that optic flow selectively activates specific regions of the visual association cortex in nonhuman primates (Duffy & Wurtz, 1991, 1997) and homologous areas in human adults (de Jong, Shipp, Skidmore, Frackowiak, & Zeki, 1994; Morrone et al., 2000). At the same time, neuroanatomical (Huttenlocher, 1990; Huttenlocher & Dabholkar, 1997), neurophysiological (Chugani, Müller, & Chugani, 1996; Chugani & Phelps, 1986), and behavioral (Atkinson, 1984; Bronson, 1982; Johnson, 1990) evidence suggests that many cortical areas, including primary visual cortex and the dorsal stream systems to which it projects, may not be functionally mature at birth but instead develop rapidly over the first several months of life. Accordingly, infants' discrimination of changes in heading direction may be slow to develop in part because of prolonged patterns of maturation in dorsal stream circuits that are specialized for optic flow processing.

In conclusion, the current experiments provide new data concerning whether 3- to 6-month-old infants discriminate between optic flow patterns that simulate different directions of self-motion. Consonant with previous results (Gilmore & Rettke, 2003) obtained with 4-month-olds only, these findings suggest that prelocomotor infants discriminate between optic flow patterns only when large changes in heading angle are simulated. The results provide evidence consistent with that of other research that many dimensions of spatial perception (Atkinson, 2000; Banton et al., 2001) and cognition (Newcombe & Huttenlocher, 2000) develop

over many months in infancy because of both the nature of infants' own visual experiences and changes in the underlying neural substrates that link perception and action. What specific sources of visual information underlie infants' performance, when adultlike sensitivity emerges, and what other factors influence its emergence remain questions for future research.

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Received May 30, 2003

Revision received October 20, 2003

Accepted October 27, 2003 ■