

Convergence and divergence to radial optic flow in infancy

Elizabeth Nawrot

Department of Psychology, Minnesota State University
Moorhead, Moorhead, MN, USA



Mark Nawrot

Center for Visual and Cognitive Neuroscience,
Department of Psychology, North Dakota State
University, Fargo, ND, USA

Research finds a relationship between the development of depth perception and ocular motion functions including smooth pursuit and ocular following response. Infants' reactions to looming stimuli also suggest sensitivity to optic flow information that specifies relative distance. With radial optic flow, an expanding flow field elicits involuntary convergent eye movements while a contracting one elicits involuntary divergent eye movements. This response suggests the visual system is interpreting the radial flow as a change in relative depth. We measured the oculomotor response to radial optic flow in infants aged two to five months. The stimulus comprised a radial optic flow pattern that expanded or contracted across eight 400 ms trials while eye position was monitored with a Tobii X120 eye tracker. A subset of infants also viewed trials of a static version of the stimulus. On average, most infants in each age group demonstrated convergence to the expanding pattern and divergence to the contracting one. Moreover, the difference in gain between the convergence and divergence eye movements was significant. The presence of correct-direction vergence eye movements in response to expansion and contraction provides further evidence that infants are sensitive to information that specifies relative motion in depth.

Introduction

The infant visual system appears well equipped to respond to motion with eye movements designed to stabilize fixation, pursue moving targets, and perceive objects in different depth planes. The oculomotor system that controls vergence eye movements works to coordinate bifoveal fixation in preparation for the crucial task of binocular stereopsis that will lead to the emergence of stereoscopic depth perception around 16 weeks of age. But even earlier than this, motion-defined monocular cues are available for the developing visual system to recover information for relative depth/

distance, for example from motion parallax (Nawrot, Mayo, & Nawrot, 2009). Such cues are available in radial optic flow (ROF) patterns and may be sufficient to drive the vergence system to provide information for relative depth in the absence of accommodative change or binocular disparity. Specifically, vergence eye movements may provide information that specifies change in egocentric distance, which is the distance between an observer and a point of fixation.

Horizontal vergence eye movements change fixation from one distance to another, bringing the optical axis of the eyes closer together (convergence) or farther apart (divergence). With ROF, an expanding flow field elicits involuntary convergent eye movements while a contracting one elicits involuntary divergent eye movements (see Figure 1). Using a projected dot pattern, Busetini, Masson, and Miles (1997) demonstrated robust convergent and divergent responses that persisted under monocular viewing and even when the display was restricted to the temporal hemifields. The pattern of motion in the ROF stimulus serves as a powerful cue to a change in distance that appears to trigger a very short latency, “machine-like” vergence response (Miles, 1998). These are not contour-following slow eye movements like pursuit or optokinetic response, but instead move in the direction opposite contour movement. Moreover, these eye movements are elicited in the absence of binocular disparity change by a pattern of expansion or contraction in the visual field. This suggests that the visual system recognizes a change in distance and quickly begins to move the eyes to maintain gaze.

Infants as young as one month make vergence eye movements to both static targets and targets moving in depth with appropriate direction and adult-like sensitivity thresholds (Aslin, 1977; Aslin & Jackson, 1979; Hainline & Riddell, 1995; Slater & Findlay, 1975; Tondel & Candy, 2008). What is less clear is the mechanism that underlies the development of the vergence system, particularly the relative efficacy of

Citation: Nawrot, E., & Nawrot, M. (2019). Convergence and divergence to radial optic flow in infancy. *Journal of Vision*, 19(13):6, 1–11, <https://doi.org/10.1167/19.13.6>.

<https://doi.org/10.1167/19.13.6>

Received May 2, 2019; published November 13, 2019

ISSN 1534-7362 Copyright 2019 The Authors



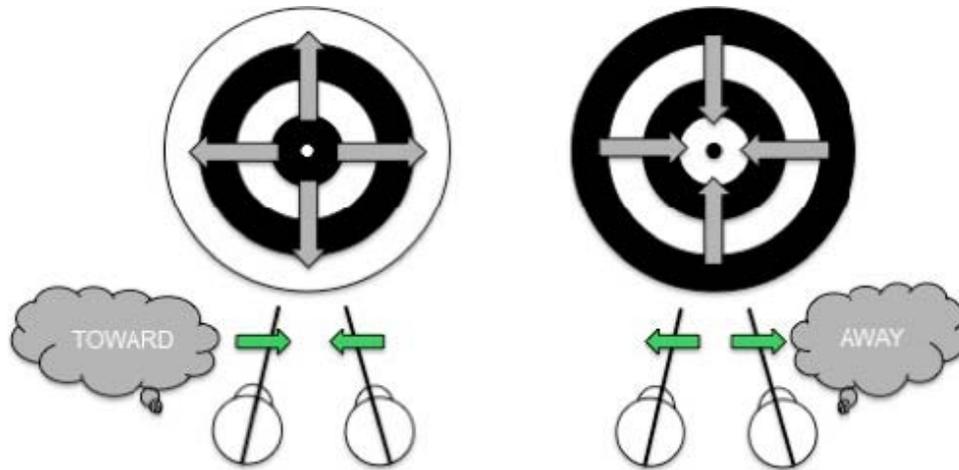


Figure 1. Predicted eye movement responses to expanding and contracting radial optic flow fields. (left) Expanding flow fields elicit convergent eye movements; (right) Contracting flow fields elicit divergent eye movements.

cues to drive vergence. The so-called near triad motor response is driven by three cues that activate vergence including the accommodative response to image blur, fusional or disparity-induced vergence, and proximity vergence (Maddox, 1893; Semmlow & Hung, 1981). Research has attempted to separate out these individual cues to assess their relative contributions during oculomotor development, especially as the accommodation and vergence response systems are linked. For example, in accommodative convergence (AC), a change in accommodation as a result of image blur is accompanied by a predictable change in vergence: An increase in accommodation evokes a convergence eye movement while a relaxing accommodation evokes a divergent eye movement. Alternately, convergence accommodation (CA) leads to a change in vergence that does not require a blur cue. The AC response can be evoked under monocular viewing as it does not rely on disparity changes (Howard, 2002).

Importantly, the infant response may not be the same as the adult response due to increased accommodation of hyperopia and smaller interpupillary distance. However, studies show that the accommodation and vergence response in infants as young as eight weeks works well to align the eyes and bring distant objects into focus (Seemiller, Wang, & Candy, 2016; Tondel & Candy, 2008). Moreover, these studies effectively isolate and examine cues from the coupled accommodation-vergence response system in order to examine their relative importance during this critical period in the developing visual system (Bharadwaj & Candy, 2008). For example, Horwood and Riddell (2013) measured changes in accommodation and vergence to targets moving in depth specified by Maddox's three cues of disparity, blur, and proximity/looming. At the youngest ages when visual acuity is not well developed, the accommodative response to blur

would be attenuated (Banks, 1980; Haynes, White, & Held, 1965). While even the newborn can exhibit binocular fixation (Slater & Findlay, 1975), it is generally accepted that sensitivity to retinal disparity for binocular depth perception does not develop before about three to four months (Birch, Gwiazda, & Held, 1982) making it an unlikely candidate to drive the vergence response in young infants. However, some recent findings may necessitate revisiting this conclusion (Seemiller, Cumming, & Candy, 2018).

Horwood and Riddell (2013) describe this situation as resulting in age-related “dead zones” for the cues of blur and disparity detection. As a result, they conclude that the proximity cues are the most effective at the youngest ages, including both static and dynamic cues such as looming, perspective, shading, and motion parallax. Similar results from Seemiller et al. (2016) lead the authors to conclude that looming cannot be ruled out as a cue to drive the vergence response in infancy.

In the absence of cues from accommodative blur and retinal disparity, Maddox's final cue is proximal vergence. The proximity vergence response is evoked from stimuli that are perceived as changing in relative distance/depth in the absence of disparity or accommodation cues (Howard, 2002). The expansion and contraction motion in ROF is a perfect example of this proximal response cue, and while Busetini et al. (1997) find vergence to ROF with adults, there is little evidence that it can drive an oculomotor vergence response in infants. The most persuasive evidence comes from studies of infants' *behavioral* responses to the expansion and contraction in ROF stimuli. The pattern of motion expansion provides potential information for impending collision and infants as young as three weeks demonstrate defensive blinking and postural adjustments in response to such stimuli (Yonas,

Pettersen, & Lockman, 1979). Moreover, sensitivity to optical expansion may develop ahead of sensitivity to contraction in keeping with this salient cue to forward motion (Brosseau-Lachaine, Casanova, & Faubert, 2008; Shirai, Kanazawa, & Yamaguchi, 2004). However, infant studies have typically used visual preferences to examine directional sensitivities or object motion coherence thresholds, while few have measured the vergence eye movement response directly.

The current study measured the direction and average magnitude of infants' oculomotor responses to expanding and contracting ROF stimuli. Previous research with adult observers used high-resolution eye-movement recordings to document the velocity profile of the vergence change elicited by the expanding or contracting stimulus (Busetini et al., 1997; Kodaka, Sheliga, FitzGibbon, & Miles, 2007). The goal of the current study was to determine only whether infant eye movements showed evidence for convergence or divergence in the brief interval following presentation of expanding or contracting stimuli. Additionally, we included a static condition with no stimulus motion in order to evaluate the possibility of spontaneous vergence eye movements. The presence of vergence eye movements in response to expansion/contraction would provide evidence that infants are sensitive to information that specifies egocentric or relative depth change and provides a possible mechanism to explain the behavioral responses found in looming studies.

Method

Participants

Infant names were identified through county birth records and newspapers birth announcements and parents were contacted either by letter or phone and invited to participate. Families were compensated with store gift cards and coupons to a local photography studio. Recruited infants were born within two weeks of due date and had no birth complications by parental report.

For the two motion conditions, data were successfully recorded from 99 infants, creating three age groups with at least 30 in each group: Two-month-olds (mean age 78.6 days, range 58–95, $n = 35$), four-month-olds (mean age 112 days, range 96–125, $n = 34$), and five-month-olds (mean age 149 days, range 126–208, $n = 30$). In the static stimulus condition, data were successfully recorded from 17 infants across the three age groups (mean age 147 days, range 63–208). Overall, data from an additional 39 infants were dropped for lack of sufficient gaze samples or equipment error. Attrition by age group was 11 (two-month-olds), seven

(three-month-olds), and 21 (five-month-olds); overall attrition in the static condition was 11. Infant attrition rates are in line with similar recent studies. Our success rate of 76% at the youngest age group compares favorably to Seemiller et al. (2016) who report a 63% success rate in infants under 10 weeks, and Horwood and Riddell (2013) who report 57% success in infants from six to seven weeks.

Materials

Stimuli were generated with Presentation® software (Neurobehavioral Systems, Albany, CA) running on an Intel Core computer (Daktech, Fargo, ND) with Windows XP (Microsoft, Redmond, WA) and were presented on a 21 in. CRT (NEC, Itasca, TX) set to a resolution of 1280×1024 pixels at 100 Hz. The monitor was positioned on a tilt-adjustable base that allowed the monitor and eye tracker to be adjusted together. Eye position was monitored with a Tobii X120 eye-tracking system (Tobii Technology, Falls Church, VA) calibrated to five points, with the control and calibration software Tobii Studio running on a separate Intel Core computer running Windows 7. A powered VGA switch allowed the CRT monitor to be driven by either computer/software system, switching between Studio for calibration and Presentation for stimulus presentation. Following calibration, the Tobii eye-tracking system sent eye position output data to both computers simultaneously via TCP/IP protocol. The experimental program running in Presentation recorded this eye position data and also used it to trigger stimulus events when needed. Tobii Studio, in one window, superimposed this eye position data upon an image of the dynamic stimulus being viewed by the infant, allowing the experimenter to monitor the infant's gaze and progress of the experiment. In another window, Tobii Studio also presented a video image of the infant from a USB camera mounted just above the eye tracker. In a third window, Studio presented a graphic representation of the tracking quality and the infant's viewing distance. A third Macintosh laptop computer was also connected to the VGA switch allowing brief cartoons to be presented to the infant before and between experiments.

The ROF stimulus comprised a concentric circular grating pattern with spatial frequency approximately 0.37 c° that expanded or contracted at a constant rate of $2.5^\circ/\text{s}$ across 400 ms trials. This expansion and contraction velocity corresponds to a movement of about 13 cm/s toward or away from the observer. The order of four expanding and four contracting trials was randomized. A single frame of this stimulus was used for the static condition. The attention getting stimulus (AGS) was a "happy-face" composed of a yellow circle,

3.5° in diameter, with two eyes and a mouth, gray in color. This stimulus was alternated with a magenta circle of the same size at 25 Hz, giving a flickering appearance. Viewing was binocular and gaze position was recorded simultaneously for the two eyes.

Procedure

After obtaining parental informed consent, the infant was seated on his/her parent's lap approximately 65 cm from the monitor face in a three-sided enclosure to minimize distraction. Testing began with the five-point calibration procedure, which used an infant-specific routine that included animated cartoon figures and sounds to direct the infant's gaze to each of the five points of the monitor. Following calibration, initiation of each trial was under automated eye control. In an attempt to maximize OFR magnitude, a saccadic enhancement procedure was employed at the beginning of each stimulus trial in both the motion and static conditions (Gellman, Carl, & Miles, 1990; Takemura & Kawano, 2006). Infant gaze was first drawn to a location 12° left or right of the stimulus center with the AGS. Following a 100 ms period with >70% valid eye track records with >50% within the AGS region, the AGS stimulus immediately moved to the center. This stimulus movement maximized the likelihood of a saccade back to the center. The first instance of binocular eye position falling within the new AGS region then triggered the movement of the ROF stimulus. Infants in the motion conditions viewed eight 400 ms trials, four each of expanding or contracting motion in random order. Infants in the static condition viewed four identical trials of the static stimulus, each 400 ms in duration.

Results

The raw data produced by the Tobii eye tracker was a horizontal and vertical, left and right eye position, in screen pixels, every 8.3 ms. The subsequent analysis used only horizontal eye position information. The vergence response was quantified by determining the infant's average response amplitude, the magnitude of eye movement over a fixed time interval (Perrinet & Masson, 2007). The four eye tracking recordings for each stimulus type (four trials of expansion, four trials of contraction, and four trials of static stimulus) were synchronized to stimulus movement initiation and averaged for each eye for each infant. The first 100 ms of the record was omitted due to the processing latency period for eye movement initiation (Busetini et al., 1997; Kodaka et al., 2007) and for the subsequent 300

ms left eye position was subtracted from the right eye position giving the vergence response. Divergence, an increasing right eye and decreasing left eye position, produced a positive slope, while convergence (decreasing right eye and increasing left eye position) produced a negative slope (see Figure 2).

Linear regression gave the average vergence velocity over the time interval. Gain was calculated by dividing this average vergence velocity by stimulus velocity (2.5°/s). Gain values illustrated here provide a useful way to represent the eye movements in response to a particular stimulus movement. For instance, a gain approaching 1 is found when eye velocity matches target velocity (e.g., pursuit). The use of gain in the present analysis underscores that the eye movements found here had much lower velocity than the velocity of the contour movement that elicited them.

To make a categorical decision on whether the infant was making a convergent or divergent response, the velocity threshold was set to 0.25°/s, which corresponded to a response gain = 0.10. Eye movement recordings that yielded vergence velocities below this threshold were characterized by conjugate version eye movements in almost any direction at a range of velocities and were categorized as “version/low response” for the subsequent analysis.

Figure 3 illustrates the proportion of infants in each age group that demonstrated vergence eye movements, that is, movements with gains greater than the -0.1 and 0.1 thresholds (velocities greater than -0.25 and 0.25°/s). Convergence velocities near zero were version or low response. For the expanding pattern we expect convergence and for the contracting pattern we expect divergence. In all three age groups, infants demonstrated the expected response of converging eye movements to radial optic flow contraction. For radial flow expansion, two of the three age groups demonstrated the expected divergence response. Infants at the youngest ages (two months) demonstrated expected divergent/convergent eye movements in both conditions. Chi-square analyses were performed on the categorical data illustrated in Figure 3 in order to compare the frequency of infants displaying convergence, divergence, or version/low response in each stimulus condition to a uniform distribution. Analyses confirmed that the frequency of results was significantly different from a uniform distribution across the three age groups for eye movement responses in both the contracting $\chi^2(4) = 26.18, p < 0.001$ and expanding stimulus conditions, $\chi^2(4) = 23.48, p < 0.001$.

Collapsed across all age groups, a majority of infants demonstrated the correct pattern of convergence to an expanding flow field (57%, $z = 1.31, p < 0.1$) and divergence to a contracting flow field (70%, $z = 4.2, p < 0.001$).

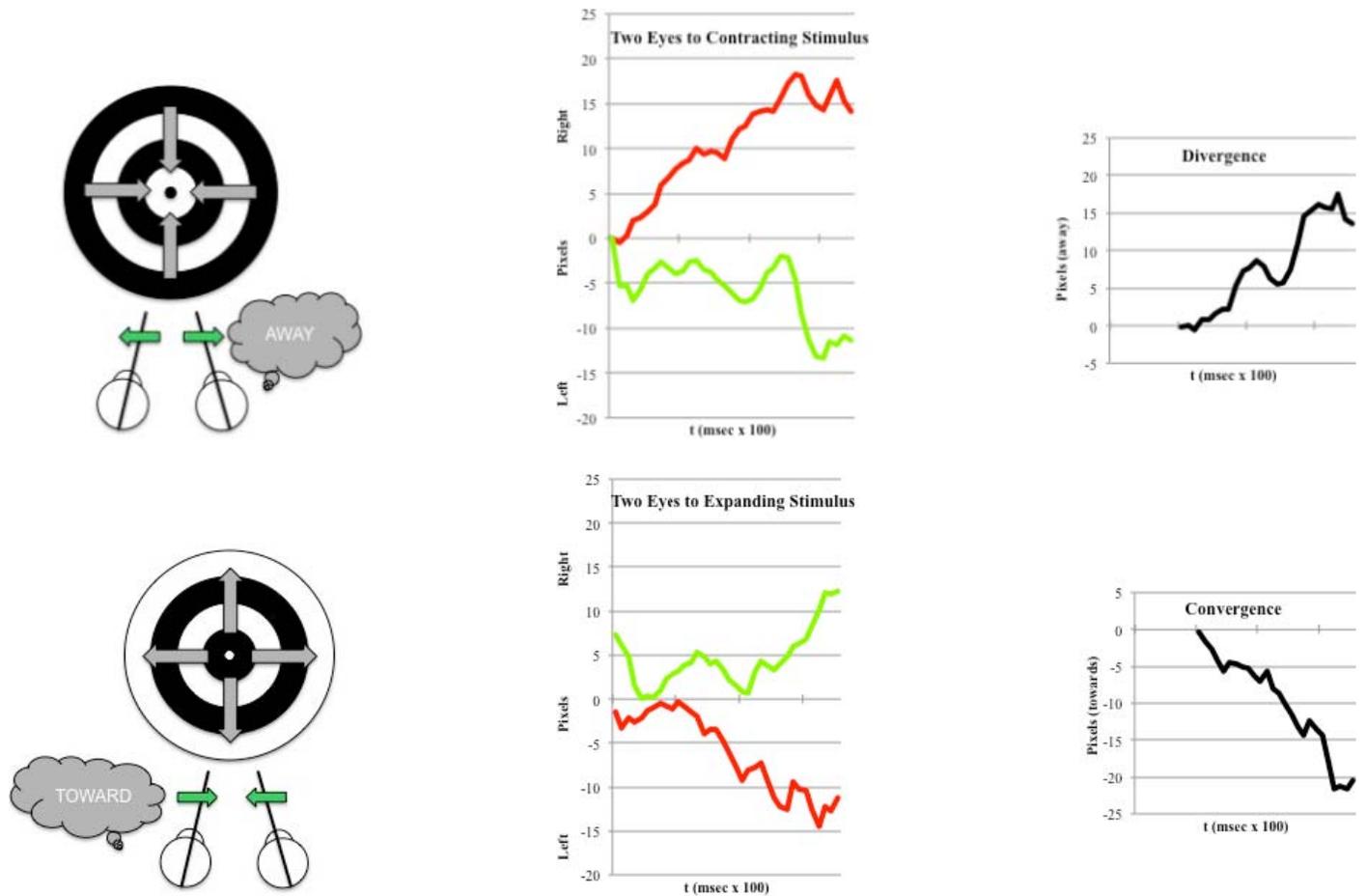


Figure 2. The figure illustrates how expanding and contracting ROF elicits convergent and divergent eye movements (right eye red, left eye green). Divergence (top panel), an increasing right eye and decreasing left eye position, produced a positive slope, while convergence (bottom panel), decreasing right eye and increasing left eye position, produced a negative slope. The vergence response was calculated as left eye position subtracted from right eye position and is illustrated by the black line tracing in the right figure panel.

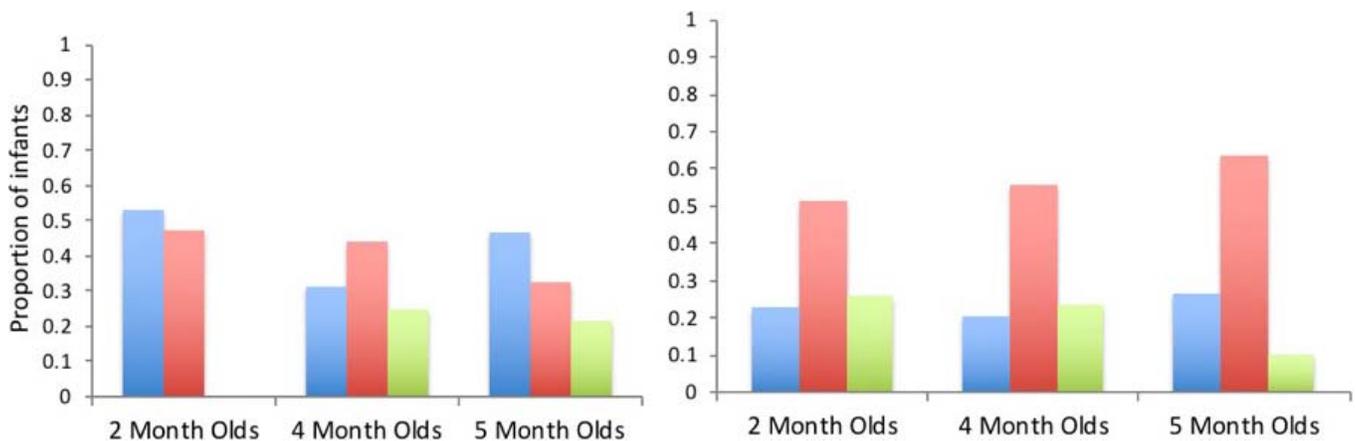


Figure 3. Bar graphs show the proportion of infants in each age group demonstrating eye movements to the two motion conditions of expansion (left) and contraction (right): Convergence eye movements are show in blue, divergence eye movements in red, and version/low response in green bars.

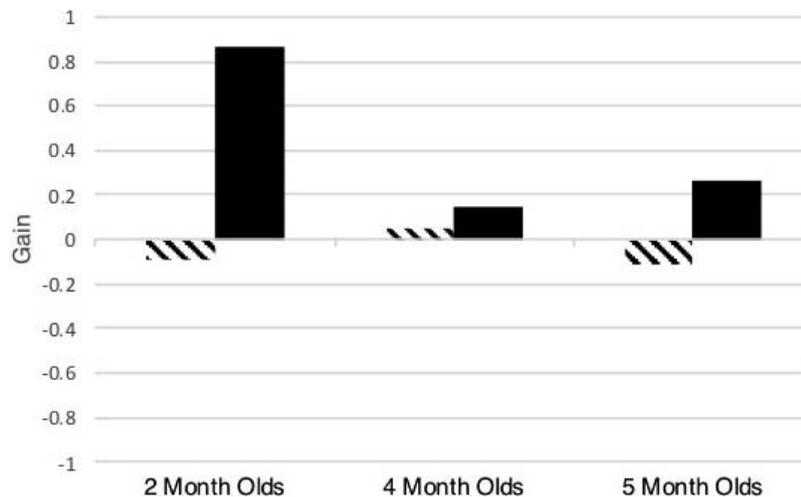


Figure 4. Illustrates the mean gain values from the expanding (hatched) and contracting conditions (solid) for each age group. Positive values indicate greater divergence as the two eyes move apart; negative values indicate greater convergence as the two eyes move closer together.

A mixed design ANOVA was computed on the vergence gain scores with age group (aged two months, three months, and five months) as the between-subjects variable and stimulus type (expansion, contraction) as the within-subject, repeated-measures variable. There was a significant main effect for stimulus type, $F(1, 96) = 16.84$, $p < 0.001$ with average gains to the contracting and expanding stimuli equal to 0.16 and -0.05 , respectively. These results indicate divergence to the contracting stimulus (as the difference between the two eyes increases), and convergence to the expanding stimulus (as the difference between the two eyes decreases). We did not make any prediction concerning the effect of age on velocity or gain values and ANOVA revealed no significant main effect for age group, $F(2, 96) = 1.91$, $p > 0.05$. However, there was a marginally significant interaction between age group and stimulus type, $F(2, 96) = 2.48$, $p = 0.09$. Figure 4 illustrates the mean gains for the two motion conditions across the three age groups.

For the static stimulus condition, Figure 5 illustrates the proportion of infants in each age group that demonstrated vergence eye movements or version/low response. The majority of infants demonstrated either divergence (red bars) or version/low response (green bars). Compared to the stimulus motion conditions, there was a similar proportion of infants that produced version/low velocity eye movements to the static stimulus illustrated by the green bars (18% of infants in the static condition compared to 15%–20% of infants in the two motion conditions). The smaller number of infants tested in this condition compared to the motion conditions prohibited a Chi-square analysis; however, a G -test of goodness of fit found no significant difference

in the number of infants producing the three different responses, $G(2) = 3.5$, $p = 0.172$.

To compare this static condition to the moving conditions, a nominal gain value was computed in the same way as in the moving conditions (vergence velocity / $2.5^\circ/\text{s}$). Using this nominal gain value, there was no significant correlation between age (in days) and gain, $r(17) = 0.04$, $p > 0.05$ (see Figure 6). Two independent samples t tests were performed to compare gain values between the static and each motion condition collapsed across age. There was a significant difference between gains from the static ($M = 0.22$) and expanding ($M = -0.05$) motion condition, $t(144) = 3.77$, $p = 0.001$. There was no significant difference between the static ($M = 0.22$) and contracting ($M = 0.16$) motion condition, $t(25.7) = 0.88$, $p > 0.05$.

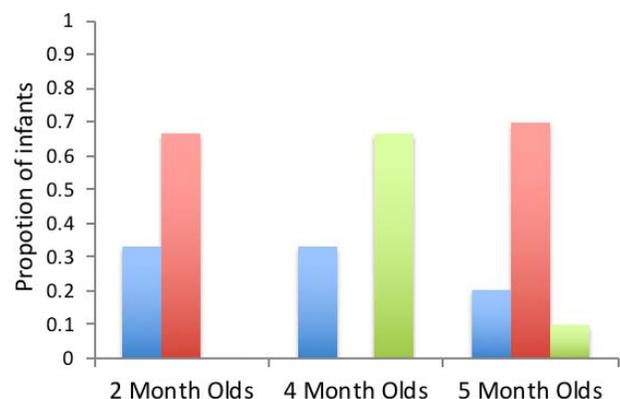


Figure 5. Bar graphs show the proportion of infants in each age group demonstrating eye movements to the static conditions: Convergence eye movements are shown in blue, divergence eye movements in red, and version/low response in green.

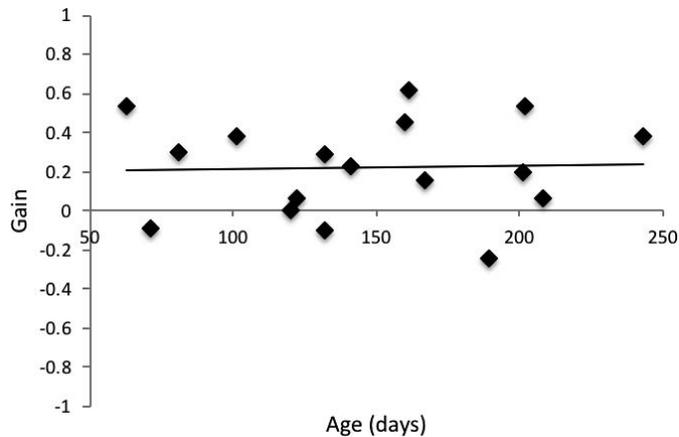


Figure 6. Gain as a function of age (in days) for infants in the static condition.

A few infants ($n = 6$) provided data in all three conditions: static, expanding, and contracting (see Figure 7). One-way repeated measures ANOVA revealed a main effect of condition (static, expanding, contracting), $F(2, 15) = 5.12$, $p < 0.05$, with mean values of 0.26, -0.23 , and 0.34 indicating the pattern of vergence eye movements in the hypothesized direction.

Discussion

We measured infants' oculomotor responses to expanding and contracting ROF stimuli from two to five months of age. We hypothesized that vergence eye movements in response to expansion/contraction would provide objective oculomotor evidence that

infants are sensitive to information that specifies change in relative distance. Results supported this hypothesis as infants demonstrated significantly different patterns of response to different directions of ROF, with an overall pattern of divergence to contraction and convergence to expansion as predicted. The contracting flow field elicited a more consistent pattern of eye movements in the predicted direction (divergence) compared to the expanding flow field (convergence). This is a compelling finding in light of previous research on infants' preference for and sensitivity to radial expansion over contraction (Brosseau-Lachaine et al., 2008; Shirai et al., 2004), although those studies did not measure eye movements per se. The results from our static, no-motion control condition bolster the conclusion that the vergence response was not simply spontaneous but due to the motion cues in the stimuli, particularly when compared to expanding motion. Data from a small number of infants tested in all three conditions was in keeping with the overall results: Contracting stimuli elicited divergence (positive slope/gain values), expanding elicited convergence (negative slopes/gain values). We did not make any specific predictions concerning the effect of age on velocity or gain for these vergence responses, unlike smooth pursuit gains, for example, that predictably increase across this age range (e.g., von Hofsten & Rosander, 1997).

This result suggests that the young infants' visual system is capable of interpreting the motion in ROF as a change in egocentric distance. This result is consistent with research on infants' behavioral responses to radial expansion, namely looming stimuli (Yonas et al., 1979). Taken together, these studies suggest that sensitivity to change in relative distance from ROF may develop very

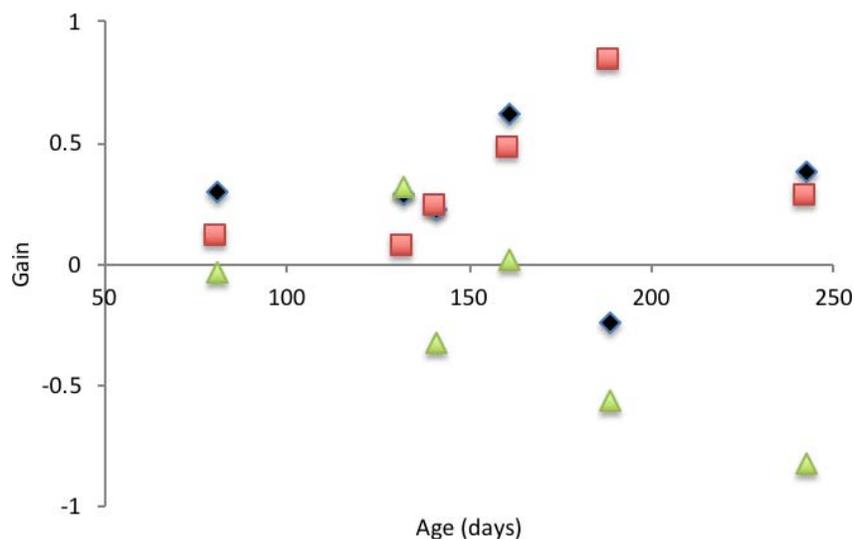


Figure 7. Gain as a function of age for six infants in the three stimulus conditions: Expansion (green triangles), contraction (red squares), and static (blue diamonds).

early. Importantly, these responses did not rely on change in binocular disparity as there was no actual distance change in the stimuli, rather the pattern of motion in the ROF was sufficient to activate the vergence response.

These findings do not suggest that ROF is the only cue capable of eliciting vergence in young infants. For example, while it is generally accepted that disparity sensitivity does not develop until about four months, some studies report limited success in demonstrating disparity sensitivity in even younger infants. Seemiller et al. (2018) reported disparity-driven vergence signals in 12 out of 16 infants under 10 weeks. Because the current experiment did not directly compare responses to ROF to those from binocular disparity or test younger infants, we cannot firmly establish the timeline where sensitivity to monocular cues develops ahead of disparity.

However, pictorially driven vergence eye movements may provide a more robust source of relative depth information in these infants compared to disparity-cues. For example, Birch and Salomão (1998) used a forced-choice preferential looking technique to demonstrate disparity sensitivity using stereoacuity cards. While the preference technique is certainly useful for clinical screenings with very young infants, it does not imply that the disparity information is driving any meaningful behavioral response. The current pattern of results demonstrating correct direction of vergence to expanding and contracting stimuli, together with research using the looming response, offers compelling evidence for relative depth perception from ROF alone.

As Howard (2002) suggested, there is a physiological substrate to support this conclusion. A number of researchers have reported neurons, particularly in cortical area MST, that respond to expansion and contraction (Duffy & Wurtz, 1991a, 1991b; Lagae, Maes, Raiguel, Xiao, & Orban, 1994; Orban, Lagae, Raiguel, Xiao, & Maes, 1995; Saito et al., 1986; Tanaka et al., 1986; Tanaka & Saito, 1989). Moreover, oculomotor responses to these ROF stimuli appear to depend, at least in part, to MST activity (Inoue, Takemura, Kawano, Kitama, & Miles, 1998) and damage to these cortical regions produces impairments in eye movements elicited by radial optic flow (Takemura, Inoue, & Kawano, 2002; Takemura, Murata, Kawano, & Miles, 2007).

The presence of convergence and divergence eye movements to ROF in the absence of disparity or blur cues is taken as good evidence for sensitivity to motion-defined change in distance (Bharadwaj & Candy, 2008; Horwood & Riddell, 2013; Seemiller et al., 2016) and is in keeping with findings of infants' sensitivity to ROF (Brosseau-Lachaine et al., 2008; Shirai et al., 2004; Yonas et al., 1979). While the acuity of the developing visual system may be limited by immaturities in

contrast sensitivity and binocularity, the oculomotor system can capitalize on dynamic, monocular cues to help recover information for viewing distance and relative depth. For example, there is growing evidence that infants less than four months old are sensitive to depth from motion parallax (Condry & Yonas, 2013; Nawrot et al., 2009; Nawrot & Nawrot, 2013; Owsley, 1983). It may be that sensitivity to monocular, dynamic depth cues develops ahead of or perhaps concurrently with the sensitivity to disparity that leads to depth perception from binocular stereopsis. Infants demonstrate precise smooth pursuit using version eye movements as well as the ocular following response (OFR) that underlies automatic saccades to reposition the eyes following translation (e.g., Nawrot & Nawrot, 2013; von Hofsten & Rosander, 1997). Infants as young as five months are also sensitive to relative motion and motion direction as cues to discriminate a variety of perceptual qualia including three-dimensional shape (Bertenthal & Bradbury, 1992; Kellman, 1984; Kellman & Short, 1987; Kellman & von Hofsten, 1992). Infants may even use the dynamic monocular cues from motion parallax to discriminate relative depth weeks earlier than disparity cues are available for depth perception from binocular stereopsis (Nawrot et al., 2009).

Horwood and Riddell (2013) emphasize a possible developmental trajectory where motion cues that signal distance and drive both accommodation and vergence develop ahead of sensitivity to binocular disparity and stereopsis. Thus, the vergence response is not dependent on the development of stereopsis, but rather it is the other way around as the motion responses serve as the “scaffold” (Horwood & Riddell, 2013). Previous research indicates that a failure of maturation of the eye movement systems may be an early step in a developmental process from strabismus to amblyopia (Braddick & Atkinson, 2011; Norcia, 1996). For example, the directional asymmetry in the optokinetic response is typical of both young infants and esotropic adults. Likewise, both populations demonstrate a deficit in depth perception from motion parallax, which relies on a smooth pursuit eye movement signal (Nawrot, Frankl, & Joyce, 2008; Nawrot & Nawrot, 2013).

Future research could directly compare the development of smooth pursuit and ocular following response to ROF to help identify early markers of visual dysfunction. The temporal properties of the two are very similar and share the same low-level local-motion energy detectors (Kodaka et al., 2007). That is, MST drives both types of eye movements and receives input from V1 and MT. It is here that the motion information is put together in different ways to drive the appropriate compensatory eye movements. This may occur in infants before the age of sensitivity to binocular disparity for depth perception, or concurrent

with disparity sensitivity given some earlier age estimates (Seemiller et al., 2018). Indeed, as Miles (1998) notes, it would be interesting to know whether OFR is affected by early disruptions of binocular vision. This is still an unanswered question with impact on the detection, diagnosis and treatment of ocular misalignments and deficits in depth perception.

Keywords: infant perception, vergence eye movements, depth perception

Acknowledgments

Portions of this research were presented at the Vision Sciences Society Meeting in Naples, FL in May, 2015, and at the European Conference on Visual Perception in Toulouse, France, 2016. The authors wish to thank Enrique Alvarez Vasquez, Dan Gu, Aubrey Borgen, Emma Johnson and the MSUM Child Development Lab, and Dr. Diana Divecha. This research was supported by NICHD R15HD058179 (E.N.) and COBRE NIGMS P20 GM103505 (M.N.).

Commercial relationships: none.

Corresponding author: Elizabeth Nawrot.

Email: nawrot@mnstate.edu.

Address: Department of Psychology, Minnesota State University Moorhead, Moorhead, MN, USA.

References

- Aslin, R. N. (1977). Development of binocular fixation in human infants. *Journal of Experimental Child Psychology*, 23(1), 133–150.
- Aslin, R. N., & Jackson, R. W. (1979). Accommodative-convergence in young infants: Development of a synergistic sensory-motor system. *Canadian Journal of Psychology/Revue Canadienne de Psychologie*, 33(4), 222–231.
- Banks, M. S. (1980). The development of visual accommodation during early infancy. *Child Development*, 51(3), 646–666.
- Bertenthal, B. I., & Bradbury, A. (1992). Infants' detection of shearing motion in random-dot displays. *Developmental Psychology*, 28(6), 1056–1066.
- Bharadwaj, R., & Candy, T. R. (2008). Cues for the control of ocular accommodation and vergence during postnatal human development. *Journal of Vision*, 8(16):14, 1–16, <https://doi.org/10.1167/8.16.14>. [PubMed] [Article]
- Birch, E. E., Gwiazda, J., & Held, R. (1982). Stereoacuity development for crossed and uncrossed disparities in human infants. *Vision Research*, 22(5), 507–513.
- Birch, E. E., & Salomão, S. (1998). Infant random dot stereoacuity cards. *Journal of Pediatric Ophthalmology and Strabismus*, 35(2), 86–90.
- Braddick, O., & Atkinson, J. (2011). Development of human visual function. *Vision Research*, 51(13), 1588–1609.
- Brosseau-Lachaine, O., Casanova, C., & Faubert, J. (2008). Infant sensitivity to radial optic flow during the first months of life. *Journal of Vision*, 8(4):5, 1–14, <https://doi.org/10.1167/8.4.5>. [PubMed] [Article]
- Busetini, C., Masson, G. S., & Miles, F. A. (1997, December 4). Radial optic flow induces vergence eye movements with ultra-short latencies. *Nature*, 390(6659), 512–515.
- Condry, K., & Yonas, A. (2013). Six-month-old infants use motion parallax to direct reaching in depth. *Infant Behavior and Development*, 36(2), 238–244.
- Duffy, C. J., & Wurtz, R. H. (1991a). Sensitivity of MST neurons to optic flow stimuli I. A continuum of response selectivity to large-field stimuli. *Journal of Neurophysiology*, 65, 1329–1345.
- Duffy, C. J., & Wurtz, R. H. (1991b). Sensitivity of MST neurons to optic flow stimuli. II. Mechanisms of response selectivity revealed by small field stimuli. *Journal of Neurophysiology*, 65, 1346–1359.
- Gellman, R. S., Carl, J. R., & Miles, F. A. (1990). Short latency ocular-following responses in man. *Visual Neuroscience*, 5(2), 107–122.
- Hainline, L., & Riddell, P. (1995). Binocular alignment and vergence in early infancy. *Vision Research*, 35(23/24), 3329–3336.
- Haynes, H., White, B. L., & Held, R. (1965, April 23). Visual accommodation in human infants. *Science*, 148(3669), 528–530.
- Howard, I. P. (2002). *Seeing in depth, Vol. 1: Basic mechanisms*. Toronto: University of Toronto Press.
- Horwood, A. M., & Riddell, P. M. (2013). Developmental changes in the balance of disparity, blur and looming/proximity cues to drive ocular alignment and focus. *Perception*, 42(7), 693–715.
- Inoue, Y., Takemura, A., Kawano, K., Kitama, T., & Miles, F. A. (1998). Dependence of short-latency ocular following and associated activity in the medial superior temporal area (MST) on ocular vergence. *Experimental Brain Research*, 121(2), 135–144.
- Kellman, P. J. (1984). Perception of three-dimensional

- form by human infants. *Perception & Psychophysics*, 36(4), 353–358.
- Kellman, P. J., & Short, K. R. (1987). Development of three-dimensional form perception. *Journal of Experimental Psychology: Human Perception and Performance*, 13(4), 545–557.
- Kellman, P. J., & von Hofsten, C. (1992). The world of the moving infant: Perception of motion, stability, and space. In C. Rovee-Collier & L. P. Lipsitt (Eds.), *Advances in Infancy Research* (Vol. 7, pp. 146–184). Norwood, NJ: Ablex.
- Kodaka, Y., Sheliga, B. M., FitzGibbon, E. J., & Miles, F. A. (2007). The vergence eye movements induced by radial optic flow: Some fundamental properties of the underlying local-motion detectors. *Vision Research*, 47(20), 2637–2660.
- Lagae, L., Maes, H., Raiguel, S., Xiao, D.-K., & Orban, G. A. (1994). Responses of macaque STS neurons to optic flow components: A comparison of areas MT and MST. *Journal of Neurophysiology*, 71, 1597–1626.
- Maddox, E. E. (1893). *The clinical use of prisms; and the decentering of lenses*. Bristol, UK: J. Wright.
- Miles, F. A. (1998). The neural processing of 3-D visual information: Evidence from eye movements. *European Journal of Neuroscience*, 10(3), 811–822.
- Nawrot, M., Frankl, M., & Joyce, L. (2008). Concordant eye movement and motion parallax asymmetries in esotropia. *Vision Research*, 48(6), 799–808.
- Nawrot, E., Mayo, S. L., & Nawrot, M. (2009). The development of depth perception from motion parallax in infancy. *Attention, Perception & Psychophysics*, 71(1) 194–199.
- Nawrot, E., & Nawrot, M. (2013). The role of eye movements in depth from motion parallax during infancy. *Journal of Vision*, 13(14):15, 1–13, <https://doi.org/10.1167/13.14.15>. [PubMed] [Article]
- Norcia, A. M. (1996). Abnormal motion processing and binocularity: Infantile esotropia as a model system for effects of early interruptions of binocularity. *Eye*, 10, 259–265.
- Orban, G. A., Lagae, L., Raiguel, S., Xiao, D., & Maes, H. (1995). The speed tuning of medial superior temporal (MST) cell responses to optic-flow components. *Perception*, 24(3), 269–285.
- Owsley, C. (1983). The role of motion in infants' perception of solid shape. *Perception*, 12(6), 707–717.
- Perrinet, L. U., & Masson, G. S. (2007). Modeling spatial integration in the ocular following response using a probabilistic framework. *Journal of Physiology-Paris*, 101(1–3), 46–55.
- Saito, H., Yukie, M., Tanaka, K., Hikosaka, K., Fukada, Y., & Iwai, E. (1986). Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. *The Journal of Neuroscience*, 6, 145–157.
- Seemiller, E. S., Cumming, B. G., & Candy, T. R. (2018). Human infants can generate vergence responses to retinal disparity by 5 to 10 weeks of age. *Journal of Vision*, 18(6):17, 1–8, <https://doi.org/10.1167/18.6.17>. [PubMed] [Article]
- Seemiller, E. S., Wang, J., & Candy, T. R. (2016). Sensitivity of vergence responses of 5- to 10-week-old human infants. *Journal of Vision*, 16(3):20, 1–12, <https://doi.org/10.1167/16.3.20>. [PubMed] [Article]
- Semmlow, J. L., & Hung, G. K. (1981). Experimental evidence for separate mechanisms mediating accommodative vergence and vergence accommodation. *Documenta Ophthalmologica*, 51(3), 209–224.
- Shirai, N., Kanazawa, S., & Yamaguchi, M. (2004). Asymmetry for the perception of expansion/contraction in infancy. *Infant Behavior & Development*, 27, 315–322.
- Slater, A. M., & Findlay, J. M. (1975). Binocular fixation in the newborn baby. *Journal of Experimental Child Psychology*, 20, 248–273.
- Takemura, A., Inoue, Y., & Kawano, K. (2002). Visually driven eye movements elicited at ultra-short latency are severely impaired by MST lesions. *Annals of the New York Academy of Sciences*, 956, 456–459.
- Takemura, A., & Kawano, K. (2006). Neuronal responses in MST reflect the post-saccadic enhancement of short-latency ocular following responses. *Experimental Brain Research*, 173(1), 174–179.
- Takemura, A., Murata, Y., Kawano, K., & Miles, F. A. (2007). Deficits in short-latency tracking eye movements after chemical lesions in monkey cortical areas MT and MST. *The Journal of Neuroscience*, 27, 529–541.
- Tanaka, K., Hikosaka, K., Saito, H., Yukie, M., Fukada, Y., & Iwai, E. (1986). Analysis of local and wide-field movements in the superior temporal visual areas of the macaque monkey. *The Journal of Neuroscience*, 6, 134–144.
- Tanaka, K., & Saito, H. (1989). Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *Journal of Neurophysiology*, 62, 626–641.
- Tondel, G. M., & Candy, T. R. (2008). Accommoda-

- tion and vergence latencies in human infants. *Vision Research*, 48(4), 564–576.
- Tsuruhara, A., Corrow, S., Kanazawa, S., Yamaguchi, M. K., & Yonas, A. (2010). Infants' perception of depth from a pictorial cue: Comparing monocular and binocular preferential-looking. *Perception*, 39, 68–68.
- von Hofsten, C., & Rosander, K. (1997). Development of smooth pursuit tracking in young infants. *Vision Research*, 37, 1799–1810.
- Yonas, A., Pettersen, L., & Lockman, J. (1979). Young infants' sensitivity to optical information for collision. *Canadian Journal of Psychology*, 33(4), 268–276.