Infant sensitivity to radial optic flow fields during the first months of life

Observations and methods

Introduction

During locomotion we perceive a large-scale pattern of visual motion called “optic flow,” which results from the dynamic projection of the visual scene onto the retina (Gibson, 1979). The analysis of this ecological motion serves important perceptual and behavioral functions, such as determining heading direction (Gibson, 1950), time to contact (Lee, 1980) and stabilizing posture (for reviews, see Duffy, 2000; Lappe, Bremmer, & van den Berg, 1999; Vaina & Rushton, 1997). Given its importance, the development of neural mechanisms mediating this type of motion information is expected to take place very soon after birth.

Several studies have demonstrated that optic flow motion information presented to the retina is processed hierarchically by mechanisms operating within area V1 and progressing to areas MT/V5, then to medial superior temporal area (MST) with progressively increasing receptive field size (Maunsell & Newsome, 1987; Tanaka & Saito, 1989; Tohyama & Fukushima, 2005). Specialized brain areas have been shown to be selectively involved in optic flow processing such as the medial superior temporal (MST) cortex in primates (Duffy & Wurtz, 1991a, 1991b; Saito et al., 1986; Tanaka, Fukada, & Saito, 1989; Tanaka et al., 1986; Tanaka & Saito, 1989) and MT+ complex in humans (Dukelow et al., 2001; Morrone et al., 2000). Behavioral data support the notion of such specialized processing as adult psychophysics’ evidenced the existence of global motion detectors with optic flow mechanisms integrating over large regions in the visual field (Morrone, Burr, & Vaina, 1995; Snowden & Milne, 1997). Evidence has also demonstrated that the coherence threshold technique may probe the higher-level mechanisms that integrate complex motion (Morrone et al., 1995).

Among the different type of optic flow-related motions expansion is of particular interest because it best defines motion during forward egomotion. The neurophysiological literature has consistently reported a directional bias for expanding motion in motion sensitive areas (Anderson & Siegel, 1999; Bremmer, Duhamel, Ben Hamed, & Graf, 2000; Geesaman & Andersen, 1996; Graziano, Andersen, 1999; Bremmer, Duhamel, Ben Hamed, & Graf, 2000; Geesaman & Andersen, 1996; Graziano, Andersen, 2000). Behavioral data support the notion of such specialized processing as adult psychophysics’ evidenced the existence of global motion detectors with optic flow mechanisms integrating over large regions in the visual field (Morrone, Burr, & Vaina, 1995; Snowden & Milne, 1997). Evidence has also demonstrated that the coherence threshold technique may probe the higher-level mechanisms that integrate complex motion (Morrone et al., 1995).

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To date, the development of mechanisms mediating translational (i.e., unidirectional) motion processing has been well documented in human infants. Starting at near birth, preferences for moving over static stimuli have been shown using preferential looking experiments (Kremenitzer, Vaughan, Kurtzberg, & Dowling, 1979; Volkmann & Dobson, 1976) with some studies demonstrating the emergence of real directional mechanisms after 2 months of age (Banton, Dobkins, & Bertenthal, 2001; Wattam-Bell, 1996a). However, relatively little is known about the development of motion-sensitive mechanisms selective to radial motion, such as optic flow, which necessitates the involvement of higher-level motion processing.

The rudimentary ability to detect motion in depth appears to emerge very early in life with defensive responses such as blinking or head movements perceived at around one month of age (Ball, Ballot, & Dibble, 1983; Ball & Tronick, 1971; Yonas, Pettersen, & Lockman, 1979) or earlier (Jouen & Lepecq, 1989). Only recently have researchers addressed the development of perceptual mechanisms mediating optic flow stimuli in infants. Gilmore, Baker, and Grobman (2004) found that the majority of infants assessed in their study were able to discriminate between optic flow displays with large changes of heading but with minimal development between 3 and 6 months. Interestingly, another group has shown that infants prefer radial expansion flow with a linear-speed-gradient over a zero-speed-gradient stimulus, and these researchers have shown an improvement of performance between 2 and 3 months of age (Shirai, Kanazawa, & Yamaguchi, 2004b).

The aim of the present study was to assess the developmental changes in radial motion sensitivity, which represents optic flow encountered during locomotion, during the first months of life. The question was one of interest in that the maturation of perceptual mechanisms was assessed prior to onset of locomotion. Instead of simple presence or absence of infants’ responses to flow information as a function of age, coherence thresholds were chosen as a measure of the cortical development of brain areas involved to optic flow processing. We believe that such a measure is more informative than looking time preferences. In the first experiment, infants’ sensitivities over a large age range were measured to assess the evolution of sensitivity over time. In a second experiment, the performance of a subgroup of infants in a longitudinal follow-up was compared. A final goal of the present study was to determine the within subject evolution of sensitivity over time for both motion directions (expanding and contracting) in order to track the developmental changes in sensitivity of these components of optic flow information.

### General method

#### Apparatus and stimuli

Stimuli were generated with the Vpixx© software (http://www.vpixx.com) and driven by a Macintosh G3 computer. Stimuli were rear-projected by an LCD projector (InFocus LP725) onto a diffused translucent screen (Da-Lite© screen), subtending 104 × 79 deg of visual angle. The image had a resolution of 800 × 600 pixels, and the refresh rate was 60 Hz. A camera was set above the center of the screen and was connected to a video recorder for on-line viewing and recordings of the participant during the experimental sessions.

During each trial, a pair of stimuli display was presented on the screen. Figure 1 demonstrates dimensions of the two stimuli displays (79 × 45 deg). Each display contained 150 bright dots (58 cd/m²) with an apparent uniform dot density (evenly distributed) on a dark rectangle region (2 cd/m²; for a Michelson contrast of 93%) on a gray background (30 cd/m²; u' = 0.1910 and v' = 0.4942).

The uniform dot density was achieved by reusing the dots that were falling off the display (“dead” dots) to fill the regions with the lowest time-averaged dot density. Therefore, the number of dots over space–time was maintained constant (see Movie). The luminance calibration was done using a Minolta Chroma Meter (CS-100). Each dot subtended 0.66° × 0.66° at the viewing distance of 57 cm. The moving dots had continuous trajectories, and each frame lasted 16.67 ms where the position of each element was updated on every video frame of the stimulus animation (60 times/sec). The incoherent dots or noise of both displays had a behavior where the dots were randomly “jittering” back and forth along its radial path. That is, each incoherent dot had a 50% chance (with replacement) of changing direction on each frame. See the Movie for alternating examples of expanding and contracting motion and the jitter noise.

One side contained coherent optic flow motion, referred to as the target display, which has a signal-to-noise ratio of varying levels. This optic flow stimulus simulated an observer traveling in translation through a circular tunnel, where the dots were randomly distributed along the walls. On the screen, the dots were moving in a radial trajectory, in expansion from the origin of motion, which was set in the center of each stimulus. The other side contained the neutral stimulus, which was equivalent to the target display in all respects (i.e., dot speed, density, radial trajectory, etc.) except for the coherence of motion, which was always set at 0% (incoherent motion or non-directional noise). This non-directional radial motion led to a planar (no impression depth or self motion) and erratic (non-directional) motion impression. The side that contained the target display was randomly selected. Non-directional radial motion has been chosen as neutral stimuli because it differed from the target
stimuli only in the global directionality of the information. Furthermore, we observed in pilot experiments that a random directional noise pattern was much more salient than the target display and the infants always looked at the control stimulus. Therefore, we used this random directional motion as the central fixation target before each trial. In order to simulate the optic flow field seen when traveling down a tunnel, dot speed accelerated with the square of the distance from the origin of expansion, or by a factor of four as the distance doubled. In this study, the dots’ speed were of $1.25^{\circ}/\text{sec}$ at an eccentricity of $5^{\circ}$ and would travel at a speed of $5^{\circ}/\text{sec}$ at $10^{\circ}$ to $20^{\circ}/\text{sec}$ at $20^{\circ}$ of his origin.

**Procedure**

During testing sessions, the infant sat on his/her parent’s lap at approximately 57 cm from the screen. In order to minimize possible distractions, the screen was surrounded perpendicularly by a wall on one side and by a gray curtain on the other. The room lighting was dimmed and the viewing was binocular. The parent was asked to simply hold their child and not take into account the stimuli presented to them during testing. A forced-choice preferential looking procedure was used to estimate the sensitivity to radial flow field stimuli varying in coherence. Before each trial, a central target (dark circle subtending $15^{\circ}$ filled with bright dots moving in random directions at a speed of $12^{\circ}/\text{sec}$) was presented at the center of the screen (gray background at 30 cd/m$^2$) in order to get the infant to fixate centrally. The use of random directional motion as a central target was motivated from a pilot study where we observed that the infants’ attention was strongly attracted by this noise stimulus. When the child was looking toward the center of the screen, the experimenter initiated the trial and the paired display was presented. The experimenter was not seen by the child and made a force choice response by judging on which side the infant gazed (eye movements, with or without direction of the head and upper body). The experimenter was blind to the stimulus presentation and viewed the gazing behavior of the infant–participant on a TV monitor that was recorded on-line by the camera. Each trial was presented until a clear gazing-behavior (right or left side) was made by the infant (usually lasting a few seconds) and was ended by entering the response. For some children, the direction of the first preferential look was consistent, but for others, both sides were compared before a final choice was made. This was qualitatively assessed in practice trials before the testing, where the experimenter observed the responses of each child while knowing on which side that target was presented. When the infant was unsettled during a trial, the trial was canceled. During the testing session, the participant and the parent took as many breaks as required. The research was approved by the institutional ethics review board of the University of Montreal. Written informed consent was obtained by the parents of all infant participants of this study before proceeding.
Experiment 1: The development of sensitivity to expanding flow fields: Cross-sectional measurements from 2 to 10 months

Participants

Infants were recruited by advertisement or from known volunteer families in the Montreal metropolitan area. All infants were born within 2 weeks of term, had an uncomplicated birth, and had no known health problems. For Experiment 1, a total of 60 healthy infants were tested. Within this group, coherence thresholds were successfully obtained for 55 of them. The other five excluded infants were either not able to complete a testing session because of crying or sleeping or manifested an asymmetrical pattern of looking (e.g., infants looking 85% of the time or more to one side were excluded). Eleven children were assessed from each of five pre-determined age groups; 2 months of age (6 male, 5 female; 8.45 weeks old ± 0.522), 4 months of age (7 male, 4 female; 17.27 weeks ± 0.647), 6 months of age (5 male, 6 female; 26 weeks ± 1), 8 months of age (7 male, 4 female; 34.91 weeks ± 0.539), and 10 months of age (4 male, 7 female; 43.27 ± 0.905 weeks of age ± SD). Testing of infants was generally completed within a single day. To ensure that each infant had normal and healthy vision, acuity was assessed with Teller acuity cards in binocular conditions (McDonald et al., 1985; Teller, McDonald, Preston, Sebris, & Dobson, 1986). If atypical visual performance was observed, infants were referred to the University Vision Clinic for a complete eye exam.

To compare the infant results to adult performance, 4 naive participants (aged 25.5 years ± 2.38) were tested under the same conditions, including practice trials with feedback to let them understand by themselves the procedure as for the infants. All adult participants had normal or corrected-to-normal acuity.

Procedure

A method of constant stimuli was used to measure the observer’s coherence threshold, i.e., the minimum proportion of dots moving in expansion that yields a coherent percept with a 75% correct response criterion. A bootstrap program (Matlab v.6.5; using a Weibull function) was used to derive the thresholds. Five pre-determined levels on a log scale were used starting at 100% coherence. The initial aim was to measure 20 trials at each level (10 “target” on each side; i.e., 10 expansion on the right side and 10 expansion on the left side) for a total of 100 trials per session per infant. Of the 55 infants where thresholds were obtained, the average number (±SD) of trials completed per infant was 83.95 (±13.24); that is, 89.0 ± 7.8 for 2 months, 84.36 ± 12.07 for 4 months, 90.9 ± 8.07 for 6 months, 78.27 ± 16.76 for 8 months, and 77.18 ± 15.04 for 10-month-old groups.

Results

Figure 2A shows the results for the Experiment 1 presenting individual coherence thresholds to expanding (outward) optic flow obtained from each participant as a function of their respective age groups. Note that thresholds for naive adults were on average lower than those

![Figure 2A](image-url)
obtained by the infants. Figure 2B illustrates the mean coherence threshold (±standard error) for each age group; 53.6% (±5.78) for 2 months; 46.62% (±6.57) for 4 months; 47.18% (±4.74) for 6 months; 29.98% (±3.45) for 8 months; and 37.13% (±3.67) for 10 months of age. The mean adult coherence threshold was 9.69% (±1.78).

Statistical analysis was carried out with the data expressed in logarithmic units. A one-factor between-group ANOVA was performed on the coherence thresholds as a function of infant age group (from 2 through 10 months). A significant age group effect ($F(4, 50) = 3.41$, $p = 0.015$) was found, and a post hoc Tukey analysis showed a significant difference between 2 and 8 months of age groups ($p = 0.014$). Other pairwise comparisons between age groups were not significant. A significant linear regression ($F(1, 53) = 7.856$, $p = 0.007$) was also present between coherence threshold and age group for infants.

A possible concern would be that our data are biased as the infants have not all completed the same number of trials. To control for this, we have calculated a weighted threshold by lumping together the individual data of all infants for each coherence level and for each given age group and then calculated the group threshold. The results are almost identical where the weighted group thresholds were 55.41%, 46.21%, 48.09%, 30.4%, and 39.2% for 2-, 4-, 6-, 8-, and 10-month-old groups, respectively (vs. 53.6%, 46.62%, 47.18%, 29.98%, and 37.13% for 2-, 4-, 6-, 8-, and 10-month-old groups).

Figure 3 shows representative psychometric functions for one individual participant for each age group.

Figure 3. Individual examples of psychometric functions with Weibull-fitted curves for each age group. Examples that were close to the mean threshold were chosen.
Despite individual variability, results revealed an improvement of optic flow sensitivity throughout the developmental period studied, particularly from ages 2 to 8 months of age. The 10-month group also had on average higher thresholds relative to the 8-month group, but this difference was not significant. Due to inherent testing difficulties for the 10-month group (i.e., lack of attention and cooperation of infants to the stimuli and procedure), we decided not to test this group in the subsequent study. In order to reduce inter-participant variability, a second longitudinal follow-up study was completed (Experiment 2, see below) that measured the optic flow sensitivity of each individual participant at different stages of development from ages 2 to 8 months.

### Experiment 2: The development of sensitivity to expanding flow fields: Longitudinal follow-up from 2 to 8 months of age

#### Methods

**Participants**

All experimental procedures were the same as in Experiment 1. A longitudinal follow-up was used with 7 participating infants (4 males and 3 females). Each participant was assessed around their 2nd (8.29 ± 0.49 weeks), 4th (17.43 ± 0.98 weeks), 6th (26.71 ± 0.49 weeks), and 8th (35.71 ± 0.76 weeks of age ± SD) month of age. Of the 7 infants followed, the average number (±SD) of trials completed per infant was 89.43 (±12.35); that is, 85.71 ± 12.26 for 2 months, 78.57 ± 12.5 for 4 months, 98.0 ± 9.29 for 6 months, and 95.43 ± 3.5 for 8-month-old groups. A complete optometric exam was performed at the University Vision Clinic for each participant to ensure normal vision at time of testing (i.e., presented no significant refractive error, pathology, or strabismus).

#### Results

Figure 4 illustrates the results for the 7 participants whose sensitivity was assessed from ages 2 through 8 months of age. Coherence thresholds for expanding flow fields for each individual as a function of their respective age group are shown in Figure 4A. One of the participants (see Participant 1 in the Participants section) showed no significant preference for the target stimulus, and therefore no threshold was obtained for the 2- and 4-month measures (plotted at 100% coherence). As a consequence, all the data from this participant were removed for the statistical analysis. However, qualitatively, this infant’s threshold decreased as a function of time (i.e., between 6 and 8 months).

Figure 4B shows mean coherence thresholds as a function of age. A one-factor, repeated-measures ANOVA performed on the infant’s log-transform data revealed a significant effect of age ($F(3, 15) = 6.674, p = 0.004$). The analysis revealed a significant improvement of performance with time ($F(1, 5) = 21.474, p = 0.006$). Overall, coherence thresholds for each child tended to decrease as a function of age. The figure also shows the discrepancy between thresholds for children and those obtained from naive adults under the same conditions.

Like for Experiment 1, “weighted” coherence thresholds were calculated and were 56.34%, 36.98%, 40.06%, and 32.34% for 2-, 4-, 6-, and 8-month-old groups, respectively (vs. 61.03%, 37.09%, 40.45%, and 34.03% for 2-, 4-, 6-, and 8-month-old groups).
Experiment 3: Longitudinal follow-up of expanding and contracting optic flow fields sensitivities

Results from both Experiments 1 and 2 demonstrated a significant improvement for the sensitivity of expanding optic flow fields during the first months of life using either cross-sectional or longitudinal approaches. Here, we addressed the specificity of the improvement of sensitivities in time, with both expansion (outward) and contraction (inward) motion. The former motion type reproduces the dynamic visual input while an observer moves forward through the environment, whereas the latter motion type reproduces the dynamic input perceived as an observer moves backward through the environment. In this longitudinal study, motion sensitivity to both directions was measured for each participant at different ages (from 2 to 8 months of age).

Methods

In this experiment, the coherence thresholds were estimated for the 2 directions of motion (expansion and contraction) for each participant. The order of presentation of the two motion conditions was counterbalanced across participants and time sessions. In order to obtain two measurements for each participant within the same testing session, a staircase procedure was used instead of the more time-consuming method of constant stimuli. Therefore, a modified 2-down/1-up adaptive staircase method (Wetherill & Levitt, 1965) was used to estimate optic flow thresholds to both expanding and contracting motion conditions, where two consecutive correct responses reduced the degree of coherence motion (%), whereas one incorrect response increased the coherence level until 10 reversals were made (or stopped after 50 trials). Threshold estimated was the average of the coherence level of the last 6 reversals. Four practice trials were presented at the beginning of each session, without reversals. The staircase started at the highest coherence (100%) and varied in log step sizes of 0.15 until there had been 4 reversals. Subsequently, the step sizes reduced to 0.075 log for the last 6 reversals. The testing lasted for 33.39 (±6.85) and 32.07 (±6.51) trials on average (±SD) for expansion and contraction conditions, respectively.

Participants

A new cohort of 7 infants (5 males/2 females) was recruited and followed longitudinally from 2 to 8 months of age (2 months, 8.57 ± 0.53; 4 months, 18.14 ± 0.9; 6 months, 27.57 ± 1.13; 8 months, 35.71 ± 0.95; weeks of age ± SD) and assessed every two months in our laboratory. Six naive adults (mean of 25 years of age ± 2.68) with normal or corrected to normal acuity were also assessed. Adult testing was done using the same procedures as that used for infants.

Results

Figure 5 shows individual results for both directions of motion (expansion and contraction) for the seven infants followed longitudinally in this experiment. Qualitatively, the data demonstrate that coherence thresholds for perceiving expanding motion were generally lower than that of contracting motion across all ages and participants. In addition, the sensitivity for contracting motion seemed to be more constant over time for most participants whereas the sensitivity to expanding motion increased with age (i.e., lower thresholds) for the majority of infants tested as was previously shown in Experiments 1 and 2.

Figure 6 illustrates the mean coherence thresholds for each direction of motion as a function of age groups. Two repeated-measure one-way ANOVAs were performed and revealed a significant main effect for the expansion direction (F(3,18) = 4.167, p = 0.021) but not for the contraction (F(3,18) = 0.616, p = 0.614), where expansion thresholds decreased with age and contraction thresholds remained stable. Pairwise planned comparisons (t-tests with Bonferroni correction, 0.05/6 = 0.008) demonstrated significant differences between the two directions of motion for the 8-month group (t = -4.674, p = 0.003). Other age groups did not reveal significant differences, considering the Bonferroni correction, despite a tendency towards significance with increasing age (2 months; t = -1.19, p = 0.279, 4 months; t = -3.196, p = 0.019, 6 months; t = -2.549, p = 0.044). In adults, mean thresholds for expansion and contraction motion did not show a significant difference (paired t-test; p = 0.357). It needs to be mentioned that the sample size was deemed to be too small for a factorial ANOVA, thereby lacking the power to detect interaction effects in the data. Therefore, planned comparisons were chosen.

In order to compare the relative rates at which the mechanisms underlying expanding vs. contracting motion develop as a function of age, sensitivity measures were normalized by expressing them in terms of relative sensitivity (dB), i.e., the mean sensitivity at each age group was calculated relative to the highest sensitivity (or lowest threshold) for each condition using the following equation:

\[
\text{dB} = 20 \times \log_{10}(S_i/S_{\text{max}}),
\]

where \(S_i\) is the sensitivity of the ith age group and \(S_{\text{max}}\) is the highest sensitivity.
where $S_i$ refers to the mean sensitivity at each age group and $S_{\text{max}}$ refers to the minimum mean sensitivity measured for each condition. For each function, 0 dB represents the age group with the highest mean sensitivity for each condition, which in the present study was found in the 8 months of age group for both motion conditions. By measuring the relative sensitivity, the relative rate of decline can be measured independently of absolute differences in sensitivity between expansion and contraction motion conditions. As demonstrated in Figure 7, the
sensitivity to contracting motion is relatively unchanged across age whereas sensitivity to expanding motion increases with age, particularly between the ages of 2 and 4 months.

**Discussion**

The present study is the first to measure motion coherence thresholds derived from psychometric functions to directional radial vs. non-directional radial optic flow patterns throughout the first months of life. Coherence thresholds were measured with preferential looking method in order to address the development of optical flow sensitivity in infants on a large extent of ages with both between (cross-sectional) and within (longitudinal) designs. Moreover, this investigation is the first to dissociate expansion and contraction coherence thresholds (not preferences) across several infant age groups.

As expected, results from Experiment 1 showed a significant and a linear improvement in optic flow sensitivity with age group, with the most significant increase occurring at about 8 months. The average decrease in sensitivity observed for the 10-month group might be explained by the uncooperative tendencies during testing such as shortened attention span, strong desire to explore surroundings other than what was presented to them and decreased ability to stay still during testing. In an attempt to reduce inter-subject variability, sensitivity was measured for a subgroup of infants at 2-month intervals for a period of 6 months (within subject design: from 2 through 8 months of age). Developmental studies often have to deal with large inter-individual discrepancies or variations, not only across age groups, but also within a specific age group. As it was found in Experiment 1, mean sensitivity improved significantly with age. However, the most significant increase occurred between the ages of 2 and 8 months for Experiment 1 but tended to increase more rapidly between 2 and 4 months in Experiment 2. The difference between the two experimental designs, i.e., between vs. within design, might explain the variation between Experiments 1 and 2. Indeed, a longitudinal design might better control for the inter-individual variations between age groups, and this might be reflected by an earlier improvement of performances. Furthermore, the similar improvement of performance with development may suggest that our longitudinal results are not the result of learning. Banton, Bertenthal, and Seaks (1999) have shown a similar developmental pattern between cross-sectional and longitudinal measurements regarding infants’ optokinetic responses to leftward or rightward global motion. With identical experimental conditions (stimuli, procedure, etc.), they have demonstrated results from between design (cross-sectional) consistent with those from the within design (longitudinal), in the development of the ability to integrate global motion direction.

The motion coherence sensitivity measures obtained in the present study seem consistent with those of Wattam-Bell (1994), although these researchers used a different task; preferential looking of horizontally translating motion stimuli. Mean thresholds were near 70%, 40%, and 5–7% for infants of 11 weeks, 16 weeks of age, and adults, respectively. An improvement in motion coherence sensitivity through time was also reported in Mason, Braddick, and Wattam-Bell (2003) using a preferential looking paradigm. This previous study found no significant improvement in optokinetic nystagmus performance.

![Figure 6](image_url)

**Figure 6.** Bar plot showing mean performance of participants for the two conditions: expansion (empty bars) and contraction (full bars) motion direction. Mean coherence thresholds are plotted as a function of age groups (+1 SEM).

![Figure 7](image_url)

**Figure 7.** Relative sensitivity (dB) for expansion (outward) and contraction (inward) conditions as a function of age tested.
but preferential looking performance improved significantly with age for coherence threshold of translational motion direction in infants between 6 and 27 weeks of age. Furthermore, this method was used to address cortical mechanisms, consistent with Mason et al. (2003) study, who suggested that the preferential looking discrimination of coherence motion depends on a cortical directionally selective system. Our results likely reflect the maturation of extrastriate cerebral visual areas subtending optic flow motion integration (e.g., human homologue of area MST) and their underlying connectivity. Banton and Bertenthal (1997) proposed that the projections from V1 to the MT/MST mature functionally around 2 or 3 months of age, reflected by the emergence of sensitivity to relative motion. The integration of local directional components required for the processing of radial motion requires higher-level processing than for simple translation motion, as defined by neurophysiological studies (Saito et al., 1986; Tanaka et al., 1989), suggesting posterior cortical areas involved in optic flow analysis.

In the context of other areas of early visual development, a relatively slow development of radial optic flow sensitivity is found compared with grating acuity, which undergoes a relatively rapid development during infancy (Skoczynski & Norcia, 1999, 2002). The rate of development of radial motion sensitivity seems to be more comparable to stereoacuity or to vernier acuity sensitivity, which are reported to show a slow improvement after a rapid emergence (Birch & Petrig, 1996; Birch & Salomão, 1998; Brown, 1997; Leat, Pierre, Hassan-Abadi, & Faubert, 2001). This slow improvement may not be complete for several years, as evidenced for vernier acuity, which is reported to be mature only around 14 years of age with VEPs (Skoczynski & Norcia, 2002). Like radial motion, development of vernier acuity is also known to be further limited by cortical factors (Levi, Klein, & Atsebaomo, 1985) and to be a more meaningful indicator of higher order visual function (Skoczynski & Norcia, 1999).

Adult performance was clearly superior to children’s for optic flow sensitivity. The gradual increase in coherent motion sensitivity between infancy and adulthood continues until it plateaus, or matures, to adult levels as demonstrated in primates (Kiorpes & Movshon, 2004) and human children with a continued improvement up to around 10 to 11 years of age (Gunn et al., 2002). At the other end of the human lifespan, studies investigating motion coherence sensitivity in non-pathological aging demonstrate that sensitivity to radial motion is selectively affected when compared to translational (unidirectional) motion information (O’Brien et al., 2001; Warren, Blackwell, & Morris, 1989).

In Experiment 3, different tendencies for the same infants that were tested with the two directions of motion were demonstrated. Our longitudinal results demonstrated superior performances for expansion direction (outward representing movement towards the observer) than for contraction direction (inward representing movement away from the observer) of radial motion. Results may suggest that the sensitivity to the direction corresponding with forward locomotion, e.g., expansion, develops at a faster rate than for the opposite direction encountered when moving backwards, or contraction. The dissociation between the directional mechanisms appears to begin as early as 2 months, but this dissociation becomes statistically significant at the age of 8 months under the experimental conditions used in our study. Consequently, coherence thresholds for expansion may be a more sensitive measure for developmental trends between 2 and 8 months. This expansion/contraction sensitivity discrepancy also validates the specificity of the observed developmental trend toward a genuine preference for optic flow motion rather than only for coherent motion over incoherent motion.

A recent preferential looking study has investigated 2 and 3 months of age infants’ preferences for radial expansion and contraction stimuli compared with a random directional pattern using a preference score, measured by the ratio of looking time for the target over total looking time (target and noise pattern) (Shirai, Kanazawa, & Yamaguchi, 2006). They showed a nonsignificant preference for either expanding or contracting radial motion over the random directional pattern (non-directional noise) at 2 months of age. However, a significant “negative preference” was found for the random motion pattern over contracting, but not expanding motion, at 3 months of age. Based on their results, they suggest that anisotropic motion coherence sensitivity to radial expansion/contraction emerges at around 3 months of age, with a contraction bias. However, we argue that the noise stimuli used in their experiment is much more salient than either of the two directional motions, particularly relative to the contraction motion (preference of random noise over radial stimuli). In fact, in our pilot experiments, we chose not to use a similar random directional stimulus because infants demonstrated greater interest to the random pattern than to the target stimulus, possibly reflecting attentional rather than directional preference. To overcome this possible methodological confound, we have used non-directional radial motion where the only difference between the target and neutral stimuli is the directionality of the information. We therefore argue that directional motion mechanisms were assessed, and not motion detection, since the form of the motion stimuli were controlled for (Hutchinson & Ledgeway, 2006; Smith & Ledgeway, 1997).

A bias for expanding optic flow patterns has been extensively reported, mostly in the neurophysiology literature. Centrifugal directional bias of visual neurons has been reported in several animal studies; a marked anisotropy in favor of directions oriented away from the center of gaze, which corresponds to the optic flow field encountered during forward locomotion (expansion of motion) (Albright, 1989; Rauschecker, von Grünau, & Poulin, 1987). A larger proportion of expansion-selective neurons compared with other direction-selective neurons is reported in specialized motion responsive areas of macaque monkeys (Anderson & Siegel, 1999; Bremmer
et al., 2000; Duffy & Wurtz, 1991a; Geesaman & Andersen, 1996; Graziano et al., 1994; Read & Siegel, 1997; Schaafsm & Duyse ns, 1996; Siegel & Read, 1997; Tanaka & Saito, 1989) and cats (Brosseau-Lachaine, Faubert, & Casanova, 2001). This bias for outward radial motion can be put in relation with the more ecological egomotion, which is mostly experienced in the forward direction, corresponding with the expansion direction.

Brain imaging in human adults have demonstrated larger activation of the visual occipito-parietal areas when stimulated with expanding compared to contracting motion (Ptito et al., 2001). However, psychophysical studies with adults have failed to find a bias for expanding motion stimuli (Beardsley & Vaina, 2005; Morrone, Burr, Di Pietro, & Stefanelli, 1999). However, Beardsley and Vaina (2005) have noted the compelling similarity between the bias for expansion in MSTd and their measured preference for radial motions. Also, anisotropic responses to motion in depth were reported in favor of an approaching motion toward the eye (Lewis & McBeath, 2004; Perrone, 1986). Finally, studies conducted with very young infants have demonstrated defensive behavioral responses to various expanding stimulus (Ball et al., 1983; Ball & Tronick, 1971; Yonas et al., 1979), suggesting that these defensive responses to looming stimuli might be mediated by sub-cortical pathway rather than a motion sensitivity elicited by cortical mechanisms (Shirai, Kanazawa, & Yamaguchi, 2004a).

Does the locomotion experience influence the development of optic flow sensitivity? In our sample, children were mostly assessed during a “pre-locomotion” stage but experienced substantial passive displacement in the rigid environment, causing optical flow in either direction. Interestingly, the majority of infants in our sample begin to experience active egomotion, such as crawling, near the 8th month period. These first active displacements in space for visually guided behavior may be put in relation with our results that have demonstrated significant differences specifically at 8 months for Experiments 1 and 3.

Moreover, a study addressed the role of locomotor experience of 9 months of age infants for their postural responsiveness to global optic flow (front wall, ceiling, side walls, and floor) with or without terrestrial information in a moving room (Lejeune et al., 2006); only a weak relation between locomotor status and movement of the floor was found. However, previous study has shown that infants with locomotor experience were significantly more physically responsive to peripheral optic flow from the side walls of a moving room than were pre-locomotor infants (Higgins, Campos, & Kermoian, 1996). However, no differences in their responsiveness were seen between groups (locomotor and pre-locomotor) to the combined movement of the front wall, the side walls, and the ceiling of the moving room. They suggested that infants have the requisite postural control to respond appropriately to optic flow prior to the onset of locomotion, but locomotor experience appears necessary to functionalize lamellar optic flow in the periphery of the optic array for postural control (Higgins et al., 1996). Furthermore, it has been shown that postural responsiveness to flow fields peaks at around 9 months of age and drops somewhat thereafter (Bertenthal, Rose, & Bai, 1997; Delorme, Frigon, & Lagacé, 1989), which reveals that more experience does not automatically translate to superior postural responsiveness.

Animal experiments have addressed whether early visual experience guides the development of the bias for a centrifugal organization of the direction preference in cat extrastriate cortex (lateral suprasylvian area) (Brenner & Rauschecker, 1990). Kittens were exposed to either expanding or contracting motions (otherwise in the dark) during their 4th to 11th weeks of life. Interestingly, their results showed that the centrifugal bias would be independent of specific visual exposure, because neurons from both groups demonstrated this bias. From their results, the authors concluded that the bias for centrifugal motion, as encountered in forward locomotion, is probably innately determined as a phylogenetic adaptation and independent of early flow field exposure.

**Conclusions**

In conclusion, the present study demonstrated the development of optic flow motion sensitivity during the first year of life. This study is the first to measure coherence sensitivity to radial optic flow, with thresholds derived from psychometric functions in infants on a large age range and with both within and between designs. Our findings demonstrate that infants can perceive this complex motion as early as 2 months of age and that the mechanisms underlying this perception matures with age, particularly for expanding radial information. Directional mechanisms for radial optic flow were demonstrated to be present around 8 months of age. Moreover, longitudinal measurements with infants have revealed different time courses in their improvement. This may be due to different developmental trends and/or visuo-motor experience. Further research will be needed to address this specific question and to assess developmental trends of optical flow perception in later childhood.

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