Development of cortical responses to optic flow

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Abstract

Humans discriminate approaching objects from receding ones shortly after birth, and optic flow associated with self-motion may activate distinctive brain networks, including the human MT+ complex. We sought evidence for evoked brain activity that distinguished radial flow from other optic flow patterns, such as translation or rotation by recording steady-state visual evoked potentials (ssVEPs), in both adults and 4–6 month-old infants to direction-reversing optic flow patterns. In adults, radial flow evoked distinctive brain responses in both the time and frequency domains. Differences between expansion/contraction and both translation and rotation were especially strong in lateral channels (PO7 and PO8), and there was an asymmetry between responses to expansion and contraction. In contrast, infants’ evoked response waveforms to all flow types were equivalent, and showed no evidence of the expansion/contraction asymmetry. Infants’ responses were largest and most reliable for the translation patterns in which all dots moved in the same direction. This pattern of response is consistent with an account in which motion processing systems detecting locally uniform motion develop earlier than do systems specializing in complex, globally non-uniform patterns of motion, and with evidence suggesting that motion processing undergoes prolonged postnatal development.

Keywords: Optic flow, Development, V5/MT+, Human, Infants

Introduction

Optic flow, the complex pattern of motion generated by a moving observer, provides rich perceptual information about the direction and speed of an observer’s motion, and the layout of surfaces in the environment (Gibson, 1966, 1979). There has been considerable progress in measuring perceptual sensitivity to optic flow (Andersen & Dyre, 1989; Stoffregen et al., 1987; Warren et al., 1988; Atchley & Andersen, 1998; Stoffregen & Riccio, 1990; Warren & Mestre, 1991; Lappe & Rauschecker, 1994; Crowell & Banks, 1993, 1996; Burr et al., 1998; Morrone et al., 1999, 2000; Rushton et al., 1999; Hanada & Ejima, 2000; Burr & Santoro, 2001b; Habak et al., 2002; Baumberger & Fluckiger, 2004; Frenz & Lappe, 2005). Computational analysis has shown that any optic flow pattern can be decomposed into a combination of elementary vector fields including expansion, rotation, translation (horizontal and vertical), and deformation (Koenderink, 1986). Whether this sort of strict decomposition applies to biological systems has not yet been resolved. However, psychophysical evidence suggests that adult observers readily distinguish between expansion/contraction, rotation, and translation (Morrone et al., 1995; Burr et al., 1998, 2001; Morrone et al., 1999; Meese & Harris, 2001; Burr & Santoro, 2001b; Habak et al., 2002; Meese & Anderson, 2002).

There is also a substantial literature describing the response characteristics of brain regions sensitive to optic flow in both monkey (Duffy & Wurtz, 1991b; Graziano et al., 1994; Lague et al., 1994; Duffy & Wurtz, 1995; Orban et al., 1995; Andersen et al., 1996; Bradley et al., 1996; Duffy, 1998; Heuer & Britten, 2004; Xiao et al., 2006) and adult human (de Jong et al., 1994; Morrone et al., 2000; Dukelow et al., 2001; Braddick et al., 2001; Kourtzi et al., 2001; Peuskens et al., 2001; Pito et al., 2001; Huk et al., 2002; Wunderlich et al., 2002; Seiffert et al., 2003; Goossens et al., 2006; Smith et al., 2006). The earliest investigations of optic flow processing in the primate revealed the existence of neurons tuned for a variety of flow patterns in dorsal portion of the middle superior temporal area (MSTd) (Tanaka et al., 1989; Tanaka & Saito, 1989; Duffy & Wurtz, 1991a, 1991b; Duffy, 1998; Duffy & Wurtz, 1995, 1997a, 1997b; Heuer & Britten, 2004). As MSTd lies downstream of motion processing area MT, and areas V3a and V1, these results and others suggested that global motion pattern extraction mechanisms followed a local to global hierarchy. Some contrasting findings have emerged (Deutschlander et al., 2004; Koyama et al., 2005), but the bulk of the evidence supports a local to global hierarchy in motion processing. For example, uniform or random motion patterns most strongly activate V1 (de Jong et al., 1994; Morrone et al., 2000; Paradis et al., 2000; Pito et al., 2001; Beer et al., 2002; Wunderlich et al., 2002).

Of particular interest for the present study, the human analog of MT/MST, called V5/MT+, responds distinctively to different
types of flow (Morrone et al., 2000; Rutschmann et al., 2000; Smith et al., 2006), as does human V3A (Koyama et al., 2005), regions adjacent to human V5/MT+ (Smith et al., 2006), and areas outside the conventional dorsal visual stream (de Jong et al., 1994; Ptito et al., 2001; Beer et al., 2002; Wunderlich et al., 2002). Large diameter or temporally changing patterns of flow most consistently activate human V5/MT+ (Aihfors et al., 1999; Morrone et al., 2000; Smith et al., 2006). Moreover, radial motion evokes responses different from translation (Morrone et al., 2000; Smith et al., 2006; Beer et al., 2002) or rotation (Rutschmann et al., 2000; Wunderlich et al., 2002). Expansion may also activate larger regions of cortex (Deutschlander et al., 2004), engage distinctive sub-areas of V5/MT+ (Koyama et al., 2005), and evoke larger responses than contraction (Ptito et al., 2001; Holliday & Meese, 2005). A clear question that emerges is how complex motion extraction circuitry emerges in development.

**Optic flow responses in early development**

Behavioral measures show that many species make distinctive responses to approaching objects from receding ones from shortly after birth (Schiff, 1965). Human infants are no exception (Bower et al., 1970; Ball & Tronick, 1971; Yonas et al., 1977, 1978, 1979). Neonates even show head movements linearly related to flow velocity (Jouen et al., 2000).

Responsiveness to optic flow develops rapidly. By 4–8 weeks, the approaching motion of texture elements consistent with a single depth plane evokes greater blinking and backward head movement (Nañez & Yonas, 1994), than textures generated by multiple depth planes, or by receding textures of any sort. By 3 months, infants show preferences for expanding patches in a background of contracting patches (Shirai et al., 2004a). They also show preferences for radial dot motions that include a linear speed gradient, thereby more closely mimicking actual forward self-motion, than those depicting uniform speeds (Shirai et al., 2004b). Moreover, 3-month-olds discriminate contracting displays from a random noise pattern, but do not readily discriminate expanding displays under the same conditions (Shirai et al., 2006a, 2006b). While replicating a finding in the adult literature (Edwards & Badcock, 1993), this bias toward contracting patterns contrasts with other evidence from adults. Taken together, it appears that sensitivity to several aspects of optic flow related to the discrimination of approaching objects or observer motion—radial motion with speed gradients—emerges within the first 12–14 weeks postnatal. Moreover, there is evidence for distinctive responses to expansion versus contraction.

On the other hand, this early sensitivity has limits. For example, it does not result in precocious abilities to discriminate an observer’s direction of self-motion or heading from optic flow. Infants discriminate heading changes of approximately 22° by 3 months of age, but show minimal improvement from 3 to 6 months-of age (Gilmore & Rettke, 2003; Gilmore et al., 2004). Other investigators have shown similar prolonged developmental time courses for sensitivity to uniform motion (Wattam-Bell, 1996; Banton et al., 2001). Indeed, it appears that there is a period of rapid development in motion sensitivity in the first 8 to 12 weeks postnatal, followed by a subsequent slower progression. Even by 5 years of age, motion sensitivity remains immature (Ellemberg et al., 2004, 2003). These and similar results have been used to suggest that visual functions that likely depend on dorsal stream structures may undergo prolonged postnatal development (Wattam-Bell, 1996; Gilmore & Johnson, 1997b, 1997a; Ellemberg et al., 1999; Atkinson, 2000; Ellemberg et al., 2003, 2004; Gilmore et al., 2004).

Relatively little is known about the development of brain areas associated with optic flow processing. Early reports suggested that an area analogous to MT may be one of the few regions of the human cerebral cortex that is myelinated at birth (Flechsig, 1901). In the marmoset, a new world monkey, MT neurons mature early, possibly in parallel with V1 and other primary sensory cortical areas (Bourne & Rosa, 2006). Movshon et al. (2003) also reported robust single unit responses in infant MT under anesthesia. On the other hand, fMRI data from anesthetized infant monkeys show robust activations in V1, but not MT/V5 or V4 (Kourtzi et al., 2006), and other physiological measures suggest delayed maturation of MT relative to V1 (Rodman et al., 1993; Distler et al., 1996). Dorsal stream areas show earlier metabolic increases (Distler et al., 1996) and adult-like patterns of feedforward and feedback connections (Conde et al., 1996) than do ventral stream regions like V4. Bourne and Rosa (2006) note that marmoset MST develops later than MT, and thus it is possible that circuitry for complex motion processing associated with optic flow develops late.

The existing electro-physiological data from humans supports the prolonged maturation account. Statistically reliable VEP responses to direction reversals of dots moving uniformly at 5° per second emerge at about 10 weeks of age, two weeks earlier than responses to the 20° per second speed (Wattam-Bell, 1991). Direction-reversal VEPs emerge later than orientation-reversal VEPs even under similar testing conditions (Braddick et al., 2003, 2005). Unlike the behavioral literature, there is relatively little data comparing VEP responses of infants to global patterns of optic flow where the speeds or directions are non-uniform (Shirai et al., 2006a, 2006b; Braddick et al., 2006).

**Predictions**

Based on the existing data from adults, we predicted that temporally varying optic flow patterns would evoke distinctive VEP responses for the three types of optic flow associated with movement of the observer: expansion/contraction, rotation, and translation. Further, we expected different VEP patterns to expansion than those observed to contraction, particularly over lateral channels that are likely to record activity in human V5/MT+. We also expected to find weak direction reversal responses (at the second harmonic or 2F1) to the translational (left/right) display. This prediction follows from the findings of Cornette et al. (1998) who showed weak activation of V5/MT+ to direction reversal patterns (two axes of motion) compared to patterns that shifted between four axes of motion. Based on the behavioral and VEP data in infants, we predicted robust responses to the translational (left/right) displays in infants older than 12 weeks. Regarding infants’ responses to expansion and contraction, there are two possibilities. Behavioral data suggest that distinctive VEP patterns should be evoked by different optic flow patterns in young infants. On the other hand, it is possible that infants’ responses to optic flow would be weak or inconsistent if they depend on the maturation of human MST, and other higher order motion processing circuitry that may have a prolonged developmental time course.

**Materials and methods**

**Participants**

Adults (n = 12, 19–43 years; 8 female) with normal Snellen acuity (20/20 or better) participated in a single 1.5 h testing session.
Infants \((n = 12, 19–26 \text{ weeks}, \text{mean} 24 \text{ weeks}; 3 \text{ female})\) were also tested. Infants were full-term \((39–42 \text{ weeks of gestation})\), with no reported birth defects, health abnormalities, or discernible visual deficits.

**Display**

Participants viewed a monochrome monitor at a \(1024 \times 768 \text{ pixel resolution} \) and a \(60 \text{ Hz refresh rate} \) driven by a Macintosh G4 computer using custom software \((\text{PowerDiva} 2.71)\). From the viewing distance of 60 cm, the display area was \(20^\circ \times 20^\circ \) square. Patterns of optic flow were produced by the motion of 1025 7.2 arc min white \((105 \text{ cd/m}^2)\) dots on a black \((5 \text{ cd/m}^2)\) background that simulated a \(1.5 \times 1 \times 1 \text{ m volume} \) in which the \(x, y, \) and \(z\) coordinates were mathematically wrapped, creating a three-dimensional \((3D)\) torus.

There were three different patterns of optic flow. The left/right \((\text{translation})\) optic flow pattern depicted lateral translation of the viewpoint at a simulated speed of 0.14 \(\text{ m/s}\). The rotational pattern depicted a smooth rotation around the gaze axis or line of sight centered at the middle of the monitor. The display showed alternating rotations to the left \((\text{counter-clockwise}, \text{CCW})\) and right \((\text{clockwise}, \text{CW})\), \(17^\circ\) in either direction. At the \(1 \text{ Hz} \) direction reversal frequency \((\text{see below})\), this yielded in an angular velocity of \(34^\circ\) per second. The expansion/contraction display depicted forward/backward motion of the viewpoint at \(1 \text{ m/s}\). Because the pattern of two-dimensional \((2D)\) motion was derived from the \(3D\) positions of the dots, all three display types consisted of a non-uniform distribution of speeds. Since it is impossible to equate the distribution of dot speeds when one is trying to simulate different viewpoint motions through a rigid \(3D\) environment, we opted to choose display parameters so as to approximately equate the three displays in terms of the median dot speed \((5.5^\circ \text{ per second})\). A full cycle of motion repeated at \(1 \text{ Hz} \), and subsequently we refer to this value as \(F1\). Dot positions were updated at \(30 \text{ Hz}\) subsequently referred to as \(F_{\text{update}}\). All dots moved coherently, and had lifetimes of \(5 \text{ s}\) \((150 \text{ update cycles})\) before their positions were randomly updated. Dots that moved out of view in one frame were plotted based on their wrapped \(3D\) positions, thereby ensuring a uniform number and density of dots throughout the motion cycle.

**Procedure**

Adults were instructed to fixate the center of the screen for the duration of the trial and to avoid blinking. Infants were seated on a parent’s lap. In order to ensure that infants fixated the center of the screen, a small toy was suspended on a string in the center of the string. The experimenter moved the toy during the trial as necessary to maintain the infant’s fixation near the center region of the display. Infant fixation was monitored by observing the reflection of the video monitor in the infant’s pupil. The experimenter interrupted trials with a key press when the infant lost fixation. The data from 1 s prior to the interruption was rejected and the data collection resumed 1 s after a second experimenter key press had indicated that the infant had regained fixation.

A full trial consisted of \(10 \text{ s}, \) or \(10 \text{ full cycles of motion}\). We collected 20 trials per condition from the adults and \(4–6 \text{ trials per condition from the infants}\). Trials were presented in blocks of five for the adults and two to three for the infants, with stimulus order randomized. Adults initiated trials with a button press and could interrupt or abort trials as needed. For infants, an experimenter monitored fixation to the display. Data collection proceeded only during those periods when the infant fixated the display.

**Visual evoked potential (VEP) recording**

Steady state evoked brain electrical activity was recorded with Grass gold-cup surface electrodes placed on the scalp with a conductive gel \((10–20, \text{D.O. Weaver})\). In the adults a row of five electrodes, each referenced to \(\text{Cz}\) was placed symmetrically at the level of \(\text{Oz}\). The lateral electrodes were \(3\) and \(6 \text{ cm} \) to the right and left of \(\text{Oz}\). For infants, the same electrode arrangement was used, except that the electrodes were \(1.5 \text{ cm} \) and \(3 \text{ cm} \) from \(\text{Oz}\). Electrode impedance was between \(3\) and \(10 \text{ kilo Ohms}\). The EEG was amplified by a factor of \(50000\) for the adults and \(20000\) for the infants \((\text{Grass Model 12 amplifiers with analog filter settings} \ (0.3 \text{ to } 100 \text{ Hz, measured at } -6 \text{ dB points})\). The EEG was digitized to \(16 \text{ bit accuracy} \) at a sampling rate of \(779.92 \text{ Hz}\). An automatic artifact rejection algorithm was employed. If raw amplitudes exceeded a threshold \((50 \text{ microvolts for adults, } 200 \text{ for infants})\) within a display cycle, that cycle was rejected. If more than 10% of cycles within a trial were rejected, the entire trial was rejected. Using these criteria, while some cycles were rejected within trials, no trials were rejected for any participant in either age group.

**VEP analysis**

Average VEP response waveforms were reconstructed from averaged response spectra, using the inverse Fourier transform as a digital filter. First, complex-valued spectra were calculated for each trial and these spectra were averaged coherently—combining both amplitude and phase information—over all trials within a condition. The spectra were calculated over a \(2 s\) data window using a discrete Fourier transform \((0.5 \text{ Hz resolution})\). The waveform was reconstructed by inverse Fourier transformation of all integer frequencies up to \(10 \text{ Hz}\). This filter selectively passed the harmonics of the \(1 \text{ Hz} \) stimulus frequency and eliminated activity at \(0.5, 1.5, 2.5 \text{ Hz}\), etc. as well as all activity above \(10 \text{ Hz}\). Significant differences between scalp potential waveforms were identified and localized by a permutation test based on methods devised by Blair and Karniski \((1993)\) and Nichols and Holmes \((2001)\) using a threshold \(p \text{ value of } .05\).

Spectral analysis for single observer data was performed using an adaptive filter which provided better signal-to-noise performance than the discrete Fourier transforms \((\text{Tang & Norcia, 1995})\). The first five harmonics \((1F1–5F1, 1 \text{ Hz to } 5 \text{ Hz})\) were selected for quantitative analysis. For each participant and stimulus condition, the real and imaginary spectral coefficients were averaged separately across trials, and then the amplitude and phase were calculated from these “coherently” averaged coefficients. In a similar way, amplitudes and phases were calculated for each stimulus condition by coherently averaging the spectral data across subjects. We used the \(T^2\text{circ statistic (Victor & Mast, 1991), a 2D generalization of the t-test, in order to compare mean amplitude levels in the complex domain. This test takes into account both the amplitude and phase information contained in the VEP.}

**Results**

**Motion responses: Flow reversal waveforms**

Fig. 1 shows averaged evoked responses for a single \(1000 \text{ ms} \) cycle, separated by age group and channel. The left column depicts
responses to the counter-clockwise/clockwise rotation (CCW/CW) display; the center column depicts responses to the translation (L/R) display; and the right column depicts responses to the expansion/contraction display. Each graph was computed by synthesizing waveforms from the first 10 components of the coherently averaged spectrum. The yellow shading shows time periods when the average evoked amplitudes exceed zero based on a permutation test at the \( p \) value of 0.05 level. For adults, the figure shows a number of distinct component peaks in every display condition. The translation and expansion (contraction) displays show more numerous and lengthier periods of non-zero activity, with a notable response at the end of the contraction phase that extended for \( 125 \) ms. These responses differ from the infants in several ways. While infants also show periods of non-zero activity to all three display types, infants’ responses were similar across the displays. Moreover, most of the significant activity in infants was observed over Oz and O2.

Fig. 2 compares the display conditions against one another. Like Fig. 1, it shows averaged evoked responses for a single 1000 ms cycle, separated by age group and channel. Column 1 compares left/right translation (L/R) to expansion/contraction (exp/contr). Column 2 compares counter-clockwise/clockwise rotation (CCW/CW) to expansion/contraction, and column 3 compares translation to rotation. Points of significant differences on permutation testing between condition pairs are indicated by the black bars above the traces.

Reversing the direction of motion, leads to transient evoked activity after each direction reversal. These direction reversals occur at 0 and 500 ms. However, not all direction reversals produce the same response as can be seen in the figure. Note the transition from expansion to contraction 500 ms into the cycle leads to a larger response than transitions between left and right or clockwise/counter-clockwise. The largest difference consists of a more negative response at 300–400 ms after the transition point, 800–900 ms into the complete cycle. Points of significant difference are most consistent over lateral channels, although differences between expansion/contraction and rotation are observed over PO7, O1, Oz, and O2. The L/R and CW/CCW direction reversal responses are poorly formed and do not differ from one another.

In contrast, infants’ direction reversal responses are statistically equivalent for each of the three flow types (Fig. 2, bottom). Each of the different flow types leads to a positive peak at around 150 ms following the direction reversal—at 150 ms and 650 ms into each cycle. The peak is maximal at Oz. Indeed, a striking difference between the adult and infant responses is the relative
lack of systematic evoked activity over non-central channels in infants, but widespread and strong evoked activity over lateral channels in adults.

Motion responses: Flow reversal spectra

In our displays, the direction of motion reverses twice within each full cycle. Thus, evoked brain responses to direction reversals should appear in the even harmonics of the fundamental frequency. In contrast, responses selective to one component of the motion cycle—expansion versus contraction, for example—should appear in the odd harmonics. We therefore provide a summary of the coherently averaged responses at both the odd \(1F_1, 3F_1, 5F_1\) and even \(2F_1, 4F_1\) harmonics in Fig. 3. An analysis of the coherently averaged harmonics is a stricter test than the time-domain analysis summarized in Figs. 1 and 2. If the individual harmonics have consistent phase relationships across flow types, they will result in similar waveforms when added, even if some of the individual harmonics do not achieve a pre-specified significance level. Moreover, tests of individual harmonics against zero are potentially more sensitive than tests between conditions.

Fig. 3 depicts the coherently averaged responses shown by adults (left) and infants (right) to the three different display types across the five recording channels, focusing on the five lowest harmonics (1F1–5F1). The expansion/contraction display evoked larger first harmonic (1F1) responses across all the channels except Oz, with the difference especially pronounced over channels PO7, O2, and PO8. Amplitudes to the expansion/contraction display exceeded zero, based on the \(T^2\)-circ statistic, in lateral channels PO7 and PO8, with a marginally significant result over O2. In contrast, the responses to the left/right and rotation displays showed both smaller amplitudes and minimal variation across channels at the 1F1 harmonic. None of the mean amplitudes exceeded zero for the rotation display. However, adults’ responses to the left-right display exceeded zero across all channels. Infants showed larger average responses than adults at 1F1, but their responses were more variable, and none differed statistically from zero.

Adults’ responses to the direction reversal signal in the displays, indicated by responses at the second harmonic (2F1), are shown in the second row of Fig. 3A. Here, the overall pattern of responses differs from that shown at 1F1. The highest amplitude responses are shown over central channels, especially O1, Oz, and O2, where the mean response to the expansion/contraction display exceeded zero. Marginally significant responses were observed to the translation display over Oz, O2, and PO8, and to rotation over PO8. In contrast, infants showed statistically significant 2F1 responses to translation over every channel. A marginally significant response was observed to rotation over Oz, but there was no statistically significant response to the expansion/contraction display.

The pattern of responses to the 3F1 harmonic (third row) shows even stronger differences between the conditions in adults. Mean
A  Evoked VEP Amplitudes to Optic Flow In Adults and Infants
By Harmonic and Channel

Adults (n=12)  Infants (n=12)

1F1

2F1

3F1

4F1

5F1

B

Adults (n=12)  Infants (n=12)
amplitudes to the expansion/contraction display exceeded zero in every channel. There were no significant responses to either the left/right or rotation display in any channel at this harmonic. Infants showed a significant rotation response over PO8, but no other significant responses.

Fig. 3B shows responses to the higher order harmonics, 4F1 and 5F1. In adults, responses to the 4F1 harmonic were strongest to the expansion/contraction display. Statistically significant non-zero responses were observed over all channels. Similarly, the rotation display evoked non-zero responses over Oz and O2. There was a marginally significant response to the left/right display at 4F1 over O1. Infants showed no statistically significant 4F1 response. Non-zero 5F1 responses in adults were observed only over O1 to translation and in infants over PO7 to rotation.

Motion responses: Amplitude ratios

There can be substantial individual differences in VEP amplitudes, especially among infants whose amplitudes are larger than adults to begin with. Accordingly, an alternative approach involves examining ratios of harmonic components computed within individuals, thereby normalizing results across individual variations in amplitude. This approach can also reveal age group differences, as well. In particular, if evoked activity to the expansion/contraction and translation displays differ at the odd (1F1) and even (2F1) harmonics, this should be revealed in a comparison of the relevant ratios. Fig. 4 reveals additional information about the pattern of results. Fig. 4A shows a scatter plot of the amplitude ratios observed for each participant over Oz, where both translation and...
rotation are compared to expansion/contraction. Each data point reflects an individual participants’ response. The abscissa (horizontal) axis depicts the amplitude of the response to translation divided by the response to expansion/contraction. The ordinate (vertical) axis depicts rotation amplitude divided by expansion contraction. The majority of adults’ responses at 1F1 are in the lower left quadrant. This indicates that most participants showed larger 1F1 responses to expansion than to either translation or rotation. In contrast, adults’ responses at 2F1 (Fig. 4A: right column) are shifted to the right, indicating that responses to translation were relatively higher than those to expansion at this harmonic. Infants’ responses across both harmonics are more widespread and less systematic. Some infants show adult-like amplitude ratios, but many do not.

Fig. 4B highlights the difference between 1F1 and 2F1 amplitude ratios. It shows the mean amplitude ratios (translation/expansion and rotation/expansion) for both 1F1 and 2F1. Adults show much lower amplitude ratios at 1F1 than they show at 2F1—indicating distinctive processing of expansion/contraction versus translation, whereas the difference for rotation is smaller, and not statistically significant. Infants, on the other hand, show no statistically significant differences at either harmonic or display. An ANOVA on the log amplitude ratios with age, harmonic, and display-type as factors verifies the pattern illustrated in the figure. There is a main effect of harmonic, $F(1,88) = 8.66, p = 0.004$, but no other statistically significant effects. In adults, the mean amplitude ratio for translation is smaller at 1F1 than at 2F1, $p = 0.002$.

**Update responses**

In addition, we distinguish between responses to the motion reversal (motion responses) indexed by harmonics of F1 (nF1) and those to the local displacements due to the screen update or refresh rate (update responses) indexed by $F_{update}$ (Fig. 5).

Fig. 5 shows the responses of both the adult and infant groups at the 30 Hz ($F_{update}$) dot update rate. This response is composed of an unknown mixture of local luminance/contrast responses and direction-specific responses. The figure indicates that in adults, there are far fewer differences between the displays than are present for the harmonics of the flow-related response. Non-zero responses are observed to the left/right display over PO7 (marginal) and PO8. Expansion/contraction displays evoked non-zero responses over all channels. Non-zero responses were also observed to the rotation displays over O1 (marginal), Oz, O2, and PO8. For infants, the responses were small, not systematic, and exceeded zero only for the expansion/contraction condition in channel O1. Infants have strong dot related responses at lower dot update rates (e.g., 15, 20 Hz; Hou et al., 2006).

**Discussion**

Coherent direction-reversing optic flow patterns evoked VEPs in adults that clearly distinguished between expansion/contraction, translation, and rotation in both the time and frequency domains. The contraction/expansion transition evoked a more negative response at 300–400 ms that was not present after the opposite transition or after any of the rotation or translation transition. This response asymmetry manifested itself in the presence of statistically significant responses at both the first (1F1) and third harmonics (3F1), especially in right hemisphere channels. Both spectral analysis and the reconstructed waveforms suggest that evoked responses to expansion flow patterns differ from those evoked by contraction. The expansion/contraction display also evoked second harmonic (2F1) responses over midline electrodes that were larger than for the other flow types. It is not clear what underlies this difference in direction reversal responses. A previous MEG study (Holliday & Meese, 2005) also found larger evoked responses to expansion than contraction. That study used transient presentations of dot patterns and reported differences between expansion and contraction shortly after 100 ms.

The right/left translation display evoked statistically significant activity at the first harmonic (1F1). This result is somewhat unexpected, as we neither predicted the finding, nor had an *a priori* reason to expect different responses to leftward versus rightward motion. It is conceivable that small pursuit eye movements evoked by the displays could have resulted in differences in retinal slip velocity, but it is not obvious why these tracking movements should be asymmetric, since viewing was binocular. Rotation displays evoked weak responses overall, with statistically significant activity observed only over channel PO8 at the reversal frequency (2F1).

It is also possible that the robust 1F1 differences resulted from some other, non-motion-related, signal in the displays, such as variations in luminance or contrast. Particularly, in displays with

![VEP Responses at Display Update Frequency](image_url)

**Fig. 5.** Coherently averaged spectra at the display update frequency (1F2, 30 Hz) from adult and infant participants, comparing the translation (L/R), expansion/contraction (exp/contr), and rotation (counter-clockwise/clockwise, CCW/CW) displays.
expansion and contraction, there is a risk that anisotropies in dot density, and hence luminance anisotropies, can be created, and that these differences result in the observed evoked signals. This explanation seems unlikely for several reasons. One is the particular care taken in generating the current displays. We generated dot positions in a virtual 3D environment that was the geometric equivalent of a torus in which all three coordinate axes were mathematically “wrapped.” Thus, when dots moved beyond view, they were immediately repositioned on the screen at the position that corresponded to their location in the “wrapped” 3D space. Because the dots were chosen from a uniform 3D distribution at the outset, this manipulation ensured that there were no systematic changes in the 2D projection of dots onto the viewing screen. A second reason we doubt that luminance or contrast artifacts account for the results is that data from a control study showed no systematic differences in the 1F1 response, when an observer viewed the three motion patterns through a set of filtering papers that reduced the high spatial frequency components of the motion. As a result, we believe that the results reflect differences in response to the motion patterns, not luminance or contrast artifacts.

Taken together, these results replicate other findings concerning distinctive evoked responses to expansion/contraction patterns in adults compared with translation (Morrone et al., 2000; Pito et al., 2001; Beer et al., 2002; Koyama et al., 2005; Smith et al., 2006) and rotation (Wunderlich et al., 2002; Rutschmann et al., 2000). The current results are also consistent with those showing selective activation when the direction of optic flow changes from expansion to contraction (Ahlfors et al., 1999; Morrone et al., 2000; Pito et al., 2001; Wunderlich et al., 2002) and stronger activation to expansion than contraction (Wunderlich et al., 2002; Pito et al., 2001; Holliday & Meese, 2005). The finding that direction reversal responses were weak, especially to the left/right displays replicates a similar PET result reported by Corne et al. (1998). That study found larger responses, especially in hMT+ when four axes of motion rather than two (direction reversal) was used. The weak responses to direction reversal may be due to adaptation over the 10 s trial duration.

Our results contrast with psychophysical evidence that adults have smaller coherence thresholds to contracting displays (Edwards & Badcock, 1993). Contracting displays appear to move faster than expanding ones (Geesaman & Qian, 1998), and motion aftereffects (MAEs) persists longer following contracting displays (Reinhardt-Rutland, 1994). Still, others have either found minimal or opposite biases in coherence thresholds (Morrone et al., 1999; Meese & Harris, 2001) or MAEs (Bex et al., 1998, 1999). So, the behavioral data are equivocal on the question of whether there is a bias related to expansion or contraction. This may reflect a weaker coupling between neural responses to optic flow in MST and behavioral ones (Heuer & Britten, 2004).

Infant responses

Infants’ evoked responses differed markedly from the adult pattern. While infants did show statistically significant evoked responses to the displays, especially over central channels (Fig. 1), response waveforms to all flow types were equivalent (Fig. 2). Each type of direction reversal resulted in a similar response waveform dominated by a positive peak at about 150 ms. When broken down by odd- and even-harmonics (Fig. 3), the infants showed no evidence of the expansion/contraction asymmetry present in the adults as activity at the odd-harmonics. The infant even harmonic (2F1) responses were largest and most reliable for the translation patterns in which all dots moved in the same direction. This pattern of response is consistent with a developmental account, in which motion processing systems detecting locally uniform motion mature earlier than do systems specializing in complex, globally non-uniform patterns of motion with evidence suggesting that motion processing and other dorsal stream functions undergo prolonged postnatal development (Ellenberger et al., 1999, 2003, 2004; Banton et al., 2001; Wattam-Bell, 1996).

Our results, however, contrast with a large literature on infants’ behavioral responses that discriminate between expanding and contracting patterns. There are a number of possible reasons why our displays did not evoke asymmetric evoked responses in infants. The specific characteristics of our displays do not seem plausible factors, however. Dot sizes, densities, average speeds, and display sizes are comparable to those used by other investigators. One might also question our use of long lifetime dots. We chose long lifetime dots to maximize the likelihood of eliciting a systematic response in infants and to avoid confounds between dot lifetime, dot update rate, and coherence. Indeed, since infants did show systematic responses to the lateral motion, the real puzzle concerns why expansion/contraction responses were weak in comparison.

It is possible that the particular reversal frequency used (1 Hz) was not optimal. Burr and Santoro (2001a) showed that adults’ sensitivity to optic flow patterns embedded in noise varied with display duration. They argued that local signals could be integrated within 200–300 ms, but global motion signals were integrated with time constants of 2–3 s. In the case of our current displays, each half-cycle was presented for 500 ms. The displays were presented without noise, but the time period of unidirectional stimulation fell well within the estimated integration time frame for local motion. This framework provides a way to interpret the infants’ responses. In the left/right displays, where infants showed systematic direction reversal (2F1) responses, all of the dots moved in the same direction although with different speeds. This global consistency in direction created motion signals of sufficient strength and duration (500 ms) to activate the corresponding local motion system, assuming it operates roughly within the adult range of parameters in the context of the approximately 5.5° per second motions presented here. However, the short periods of unidirectional motion were too short to activate infants’ cortical global motion systems. Indeed, according to this account, in order to use steady-state techniques, one might need to use direction reversal frequencies on the order of 0.33–0.5 Hz to evoke maximal responses to global motion even in adults. What reversal frequencies are optimal for evoking re-

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1In displays with limited lifetime dots, a fraction of dots move randomly (c) while another fraction (b) are repositioned according to the rule used for refreshing dots that have exceeded their lifetime. In many studies of motion coherence, these variables are often not systematically varied or considered independently even though the true proportion of coherently moving dots (c) is really a function of both values, that is c = 1 − b − a. For example, if dots have a lifetime of two frames at any frame update rate, then b = 0.5 of the dots are updated each frame. Thus, the maximum possible coherence—the fraction of dots moving systematically—would be at maximum 0.5. In our displays, a = 0 and b = 1/150, so what we call adjusted dot coherence c = .993. update rate, then b = 0.5 of the dots are updated each frame. Thus, the maximum possible coherence—the fraction of dots moving systematically—would be at maximum 0.5. In our displays, a = 0 and b = 1/150, so what we call adjusted dot coherence c = .993.
sponses in human infants and what spatiotemporal parameters characterize the development of infants’ cortical responses to local motion are open questions. VEP responses in human infants (Hou et al., 2006) and preferential looking behavior in infant monkeys (Kiorpes & Movshon, 2004) suggest that adult-like spatiotemporal tuning emerges gradually over many months. So, it is likely that infant responses to complex global motion will be influenced by developments in the spatiotemporal response profile of cortical neurons in ways that are as yet poorly understood.

Infants’ behavioral responses to optic flow might only be weakly controlled by systematic responses in extrastriate cortical motion processing circuits, such as V5/MT+. Rather, young infants’ behaviors might be controlled by parallel subcortical motion processing pathways that develop relatively early. Motion direction and speed discrimination can occur in adults with damaged primary visual cortices (Benson et al., 1998; Vaina & Rushton, 2000), and one basis for this may be a projection from the pulvinar to MT that develops early (Bourne & Rosa, 2006). Moreover, some neuroimaging studies (Beer et al., 2002) show activation in midbrain tegmental regions when observers view optic flow patterns. Indeed, substantial evidence (Giolli et al., 2005) from non-human animals suggests that the accessory optic system (AOS) participates in the extraction of motion signals related to self-motion and in eye, head, and body movements in response to self-motion. In turn, multiple lines of evidence suggest that developmental changes in many aspects of infant vision are consistent with a transition from subcortically to cortically dominated processing (Bronson, 1974, 1982; Atkinson, 1984, 2000; Johnson, 1990; Gilmore & Johnson, 1997a, 1997b; Braddick et al., 2003). The precise generators of infants’ VEP responses cannot be determined from this study, but most investigators assume that scalp recorded potentials record largely or exclusively cortical activity. The behavioral and VEP data may be reconciled if infants’ behavioral responses to optic flow are driven largely by subcortical systems, like the AOS. Furthermore, individual differences in the rates of cortical development may make the evoked responses of some infants detectable at different ages. Alternatively, infants’ behavioral responses could be controlled by other cortical areas that respond to flow, such as the FEF (Xiao et al., 2006). Future studies that studied both short-term stability and longer-term changes longitudinally or used wider electrode arrays would help address these possibilities.

In conclusion, these data are among the first of their kind to compare evoked cortical responses to complex patterns of optic flow in adults and infants. The adult results are consistent with a relatively large literature in adult psychophysics and brain imaging concerning the special status of expanding patterns in the visual system and provide a useful comparative benchmark for this, and future studies on the development of optic flow processing. The infant results are clearly more surprising given the existing behavioral literature, but they are in line with a growing consensus that many features of the mature visual system, especially those closely associated with dorsal stream processing, undergo prolonged periods of postnatal development. In the case of the complex, global motion processing involved in the perception of optic flow, the developmental trajectory of motion processing cells in V1 may be a critically limiting factor for the emergence of higher order systems in the V5/MT+ complex. At the same time, earlier maturing subcortical systems may play a vitally important role in mediating adaptive behavior during the period in which cortical systems are gradually developing functional responses.

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References


